Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae) in Western North America, with emphasis on species of the *hubbsi* group.

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ABSTRACT

Twenty-eight new species of the Holarctic, freshwater amphipod genus *Stygobromus* are described from a variety of subterranean groundwater habitats in western North America, including caves, springs, wells and the hyporheic zone, and new data are given on species previously described from this region. A total of 53 species are covered in this study, 44 of which are members of the *hubbsi* group. Twenty-three of the newly described species are assigned to this large species group, which is distinguished by the absence of sternal gills (processes). A phylogenetic analysis affirms the monophyly of the *hubbsi* group and suggests that a relatively strong clade of 10 species exists in the far western states of California, Oregon and Washington. A taxon-area cladogram reveals a moderately strong relationship between terminal taxa and physiographic provinces, which are designated as areas in the analysis. In contrast to eastern North America, where many distinct species groups of *Stygobromus* are recognized, taxonomic diversity is significantly reduced among the western species. A majority of species of *Stygobromus* in western North America, especially those in the *hubbsi* group, are closely similar morphologically, leading to the conclusion that many of them are derived from a common ancestor formerly widespread across much of the region.

INTRODUCTION

Species of the large, widely distributed freshwater amphipod genus *Stygobromus* are recorded from a variety of subterranean groundwater habitats, including especially caves, wells, springs and the hyporheic zone beneath surface streams. All members of the genus are stygobites (= stygobionts), inasmuch as they are restricted to subterranean waters (or their resurgence) and are characterized morphologically by loss of eyes and pigment and sometimes by attenuation of the body. *Stygobromus* belongs to the Holarctic amphipod family Crangonyctidae, which contains six extant genera and 152 described species (plus many undescribed). Although members of the family occur in both North America and Eurasia, crangonyctids are far more common and significantly more diverse in North America than in Eurasia. Approximately 80 percent of the species in the family are stygobites, and three of the six genera are exclusively subterranean (Holsinger 1994a).

Prior to publication of the present paper, *Stygobromus* included 101 described species, 98 of which were recorded from subterranean habitats in North America. Outside the continent, two species of *Stygobromus* were reported from central Asia and one from extreme eastern Europe near the Caspian Sea (Holsinger 1987; Kulkina 1992). In this paper, we describe 28 new species from the Cordilleran region of western North America and provide brief synopses for 24 species previously described from this region. We also include *S. putealis* (Holmes) from eastern Wisconsin, which, while occurring far outside the western Cordillera, is morphologically very similar to many species in the west. A majority of species (44 of 53) treated in this paper, including *S. putealis*, are assigned to the *hubbsi* group, which is a large complex of closely similar species erected earlier by Holsinger (1974) to encompass all species in the genus that, with one exception, lack sternal gills (or processes) on the pereonites. A revised diagnosis of the group is given below. The description of 28 new species of *Stygobromus* from western North America, 23 of which are assigned to the *hubbsi* group, brings the total number of described species in the genus to 129. Soon to be added to this total are descriptions of 22 more new species from central and east-central North America that are pending publication in another paper (Holsinger, ms.).

The first comprehensive taxonomic study of western North American species of *Stygobromus* was by Holsinger (1974). In that paper, 17 new species were described from Arizona, California, Orgeon, Montana, Nevada, and Washington and the previously described *S. hubbsi* Shoemaker, 1942 from Malheur Cave in Oregon was partly redescribed. Between 1974 and the present time, six more species were described from western North America. These descriptions included three species from hyporheic habitats and a spring in Colorado by Ward (1977); one species from a cave and one from a spring in the Canadian Rockies of Alberta, respectively, by Holsinger (1980) and Bousfield and

Holsinger (1981); and one species from caves on Vancouver Island, British Columbia by Holsinger and Shaw (1986, 1987). In addition, the monotypic genus *Stygonyx*, a morphologically closely similar sister genus of *Stygobromus*, was described from a phreatic water habitat in northern Oregon by Bousfield and Holsinger (1989). Two undescribed (non-*hubbsi* group) species have also been discovered in Alaska in recent years (see Holsinger et al. 1997) but will be described in another paper.

The principal objectives of the present study are: (a) to describe 28 new species of *Stygobromus* that have been discovered in groundwater habitats of western North America in recent years, primarily during the last two or three decades; (b) update taxonomic and distributional data on previously known species from this region; (c) further clarify the taxonomic and geographic limits of the *hubbsi* group species vis-a-vis other (non-member) species from western North America; (d) conduct a cladistic analysis with the dual purpose of sorting out phylogenetic relationships among western species of *Stygobromus*, especially in the *hubbsi* group, and examining the relationship between phylogeny and geographic distribution; and e) formulate a plausible hypothesis that explains the geographic distribution of numerous, morphologically closely similar stygobitic species over a large part of the highly varied and rugged terrain of the western Cordillera of North America.

We have included distribution maps for all western species of *Stygobromus*, and a table showing the frequency of occurrence of species in different kinds of subterranean groundwater habitats. A phylogenetic analysis was conducted, and the alignment of species in this paper follows the sequence established on the cladogram in which characters are partially weighted and ordered. This cladogram is also converted to a taxon-area cladogram in an attempt to examine the relationship between clades and their geographic distribution. Species assigned to the *hubbsi* group are listed first in the Systematics section, followed at the end of the section by nine non-*hubbsi* group species.

ACKNOWLEDGMENTS

We are grateful to the many biologists who assisted with the fieldwork and/or donated specimens for study. We also thank those collectors who furnished us with pertinent ecological data from their field notes. Although we have credited all those who assisted with collections of material in the "materials examined" sections under the various species, we are especially grateful to the following biologists who provided us with substantial numbers of specimens and detailed information on the habitats they sampled: Cheryl B. Barr, Andrew Boulton, Steven P. Canton, Jim Chester, Greg W. Courtney, Scott J. Harden, David B. Herbst, Ibrahim Mohammad, Marilyn Myers, Steward B. Peck, Margaret E. Ver Hey, D. Craig Rudolph, and James V. Ward.

In addition to the collectors, we thank the following museums for lending us additional pertinent materials: Bernice P. Bishop Museum (MBB), Canadian Museum of Nature (CMN), Essig Museum of Entomology (EME) of the University of California at Berkeley, Montana Entomology Collections (MTEC), Museum of Southwestern Biology (MSB), and Thomas Burke Memorial Washington State Museum (TBMWSM). Drs. Kent E. Carpenter and James D. Thomas read the manuscript and made a number of helpful comments on the phylogenetic analysis and interpretation of the results. Dr. Thomas also commented on the taxonomy and made several useful suggestions. We are especially grateful to Dr. E. L. Bousfield for encouraging us to publish our manuscript in Amphipacifica, and for his valuable editorial assistance and many useful suggestions regarding arrangement of the figures. His comments and suggestions, along with those of Drs. Carpenter and Thomas resulted in significant improvements of the paper. We also owe a special debt of gratitude to Donald Emminger of the Graphics Office at Old Dominion University for his professional assistance with preparation of the distribution maps.

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METHODS AND MATERIALS

Conventional methods for collecting subterranean amphipods have been discussed in previous papers (Holsinger 1967, 1972). Additional comments on collecting methodology as it applies to certain conditions in western North America are found in Ward (1977) and Ward and Holsinger (1981). In the laboratory all measurements were made in millimeters to the nearest tenth with the aid of a calibrated micrometer disc. Total length refers to the length of the body excluding appendages, i.e., length from base of anten-

na 1 to base of telson. The figures were prepared with the aid of a Leitz drawing tube from appendages mounted in Faure's mounting medium (a modification of the conventional Hoyer's medium) on glass slides. Drawings were sometimes made from appendages mounted in undiluted glycerin, in which case these structures were later moved to the more permanent Faure's medium for further clearing and storage. Appendages were not drawn to any particular scale unless noted to the contrary. A legend for figure symbols is provided on page 147.

With the exception of one species, holotype specimens of species described in this paper are deposited in the National Museum of Natural History (Smithsonian Institution) under the catalog numbers of the former United States National Museum (USNM). The exceptional holotype is deposited in the Canadian Museum of Nature collections (CMNC). Collections deposited in other museums are indicated by the museum abbreviation given above under "Acknowledgments". All other specimens examined in this study pertaining to the new species are designated as paratypes and are deposited in the research collection of the second author (JRH) at Old Dominion University. This material will eventually be transferred to the Smithsonian Institution.

In species descriptions, nomenclature for setal patterns on segment 3 of the mandibular palp follows the now widely used standard introduced by Stock (1974) (see Koenemann & Holsinger 2001, fig. 2g, for a recent application). According to this convention, the five different sets of setae that may occur on this segment and are designated by upper case letters A, B, C, D, and E. For the species treated in this paper, as well as most other species of *Stygobromus*, D (row of short setae on inner margin) and E (cluster of longish setae on apex) are the most common and are always present, B and C are less common and often absent, whereas A is almost always absent.

Because vandalism and pollution have become major threats to many cave habitats, we have elected to protect these sensitive environments from further destruction by providing only the name, and a very general location, of caves listed in the "material examined" sections for each species. This protocol applies only to caves, inasmuch as springs, hyporheic habitats, wells, etc. are generally less vulnerable to vandalism or frequent visitation. Thus, if there is legitimate need for a precise cave location, such information can be obtained either from a published state speleological survey (available for some states) or the JRH database upon request. State cave surveys have been published for California (Halliday 1962), Colorado (Parris 1973), and Washington (Halliday 1963). Additional information is available on caves in Oregon (Greeley 1971), and supplementary information on Washington caves was published in the "Guidebook of the 1972 Convention of the National Speleological Society."

SYSTEMATICS

Stygobromus Cope

Stygobromus Cope, 1872:422; *Aprocrangonyx* Stebbing, 1899:422; *Stygonectes* W. P. Hay, 1903: 430; *Synpleonia* Creaser, 1934:1.

Diagnosis. A recent, detailed diagnosis of *Stygobromus* is that of Holsinger (1978). However, the principal diagnostic character of the genus is the uniramous third uropod (U3), in which the ramus is 1-segmented, shorter than the peduncle, sometimes vestigial or absent, and when present armed with 1 to several short spines. The taxonomic and geographic relationship of *Stygobromus* to other genera in the family Crangonyctidae is discussed by Holsinger (1986a, 1986b).

The *hubbsi* group

Diagnosis. Distinguished from all other members of the genus *Stygobromus* (with the exception of one aberrant species in North Carolina) by the absence of sternal gills (processes) on the pereonites and the following combination of characters: mature females larger than mature males; propod of gnathopod 2 usually larger than, but sometimes subequal in size to, propod of gnathopod 1; posterior margin of propod of gnathopod 1 typically shorter than palm, usually without setae but sometimes with few short, submarginal setae just proximal to the defining angle; shape of bases of pereopods 5, 6 and 7 variable but often relatively narrow and not much expanded posteriorly, and often lacking distinct distoposterior lobes; telson usually as long as broad or little longer than broad, apical margin typically with shallow notch.

Stygobromus saltuaris, new species
(Fig. 1)

Material examined. OREGON. Lane Co.: hyporheic/seep area, Trail Creek, Willamette National Forest, HOLOTYPE ♀ (on slide mounts in part) (CMNC 2001-0020), 1 ♀ paratype (CMNC 2001-0021), G. W. Courtney, 25 June 1987.

Diagnosis. A medium-sized hyporheic species, related to *S. oregonensis* in structure of pleonal plates but distinguished by the following: gnathopods 1 and 2 with proportionately longer posterior margin; palm of gnathopod 2 concave; uropod 1 and 2 with fewer long and stout spines on rami and peduncle; uropod 3 peduncle broad; and telson lacking notch and with fewer spines. Largest ♀, 5.0 mm; ♂ unknown.

Female. Antenna 1: 66 percent length of body, 80 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 4 plumose spines; palp segment 2 with row of 2 rather long setae on inner margin; palp segment 3 bearing 1 B seta, 4-5 C setae, few D setae, and 3 E setae, lacking A setae. Inner lobes of lower lip absent. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 4 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 8 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 3 plumose spines, and 3 naked setae apically, and 1 stiff setae on inner margin; outer plate with short setae on inner margin and 1 small bladelike spine on or near apex.

Gnathopod 1: propod shorter than that of gnathopod 2; palm straight or slightly concave about 2 times longer than posterior margin, armed with 13-14 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin without setae; 4 superior medial setae; 2 or 3 inferior medial setae; dactyl nail rather long; coxa about as broad as deep, margin with 2 setae. Gnathopod 2: propod subrectangular, 2 times longer than broad; palm slightly concave medially and armed with 13 spine teeth in double row; defining angle with 2 spine teeth of unequal length on outside, 2 shorter spine teeth on inside; posterior margin approximately 70 percent length of palm, with 3-4 sets of doubly inserted setae; 6 superior medial setae, singly inserted; 3 singly inserted inferior medial setae; coxa little broader than deep, margin with 4 setae.

Pereopods 3-4: coxal plates about as deep as broad, margins with 3 setae. Pereopod 6 little longer than pereopod 7, about 55 percent length of body, and 22 percent longer than pereopod 5. Pereopods 5-7: bases of about as broad proximally as distally; posterior margins convex; distoposterior lobes well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively elongate, that of pereopod 6 about 25 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates slightly expanded distally.

Pleonal plates: posterior margin of plates 1 and 2 slightly concave or nearly straight, with 1 setule near distoposterior corner, that of 3 convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 4 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 7 spines; outer ramus with 6 spines; peduncle with 6 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 7 spines; outer ramus with 4 spines; peduncle with 4 spines. Uropod 3: peduncle usually not bearing small setae; ramus approximately 50 percent length of peduncle, with 3 apical spines.

Telson approximately 30 percent longer than broad, narrowing distally; apical margin with tiny median notch between spine clusters, bearing 10 relatively long spines.

Distribution and ecology. This species is only known from its type-locality, the elevation of which is about 640 m above sea level (G. W. Courtney, pers. comm.). The larger female (5.0 mm) in the series of two has setose brood plates.

Etymology. The epithet *saltuaris* is from the Latin, meaning "forest," in reference to the location of the type-locality in the Williamette National Forest.

Stygobromus rallus, new species
(Figs. 2, 3)

Material examined. WASHINGTON. Whitman Co.: Rock Lake Spring, about 28 km S. of Cheney, HOLOTYPE ♀ (USNM 1000069), 3 ♂♂ and 3 ♀♀ paratypes, 2 juvs., I. Mohammad, 2 July 1992; Spokane Co.: Millers Spring No. 2, 2 ♂♂, 2♀♀, I. Mohammad, 5 Dec. 1992.

Diagnosis. A relatively large groundwater species, closely related to *S. duplus* in gnathopods and uropods 1-2, but distinguished from that species as follows:

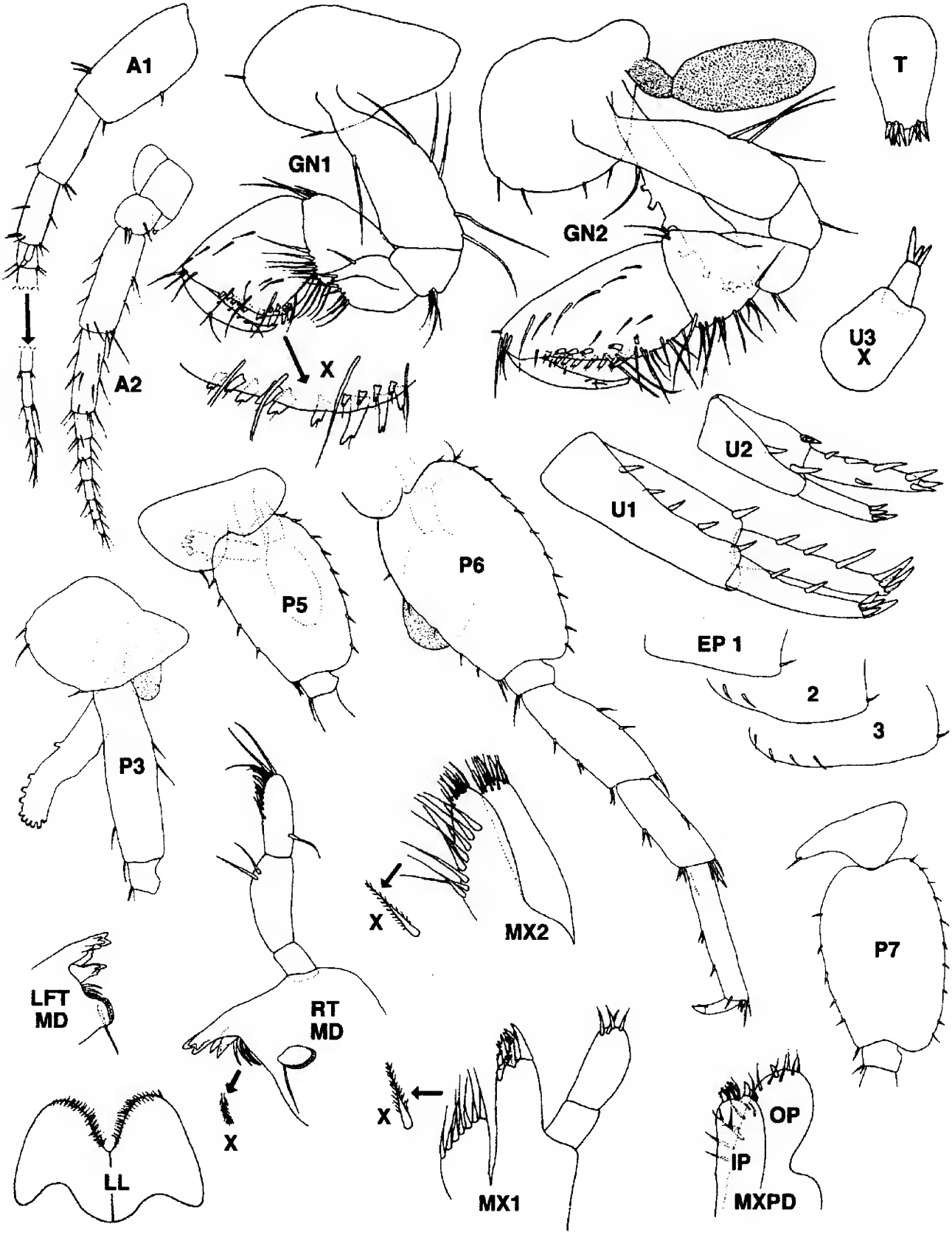

Fig. 1. ***Stygobromus saltuaris*, n. sp.** Female (4.7 mm). Lane County, Oregon.

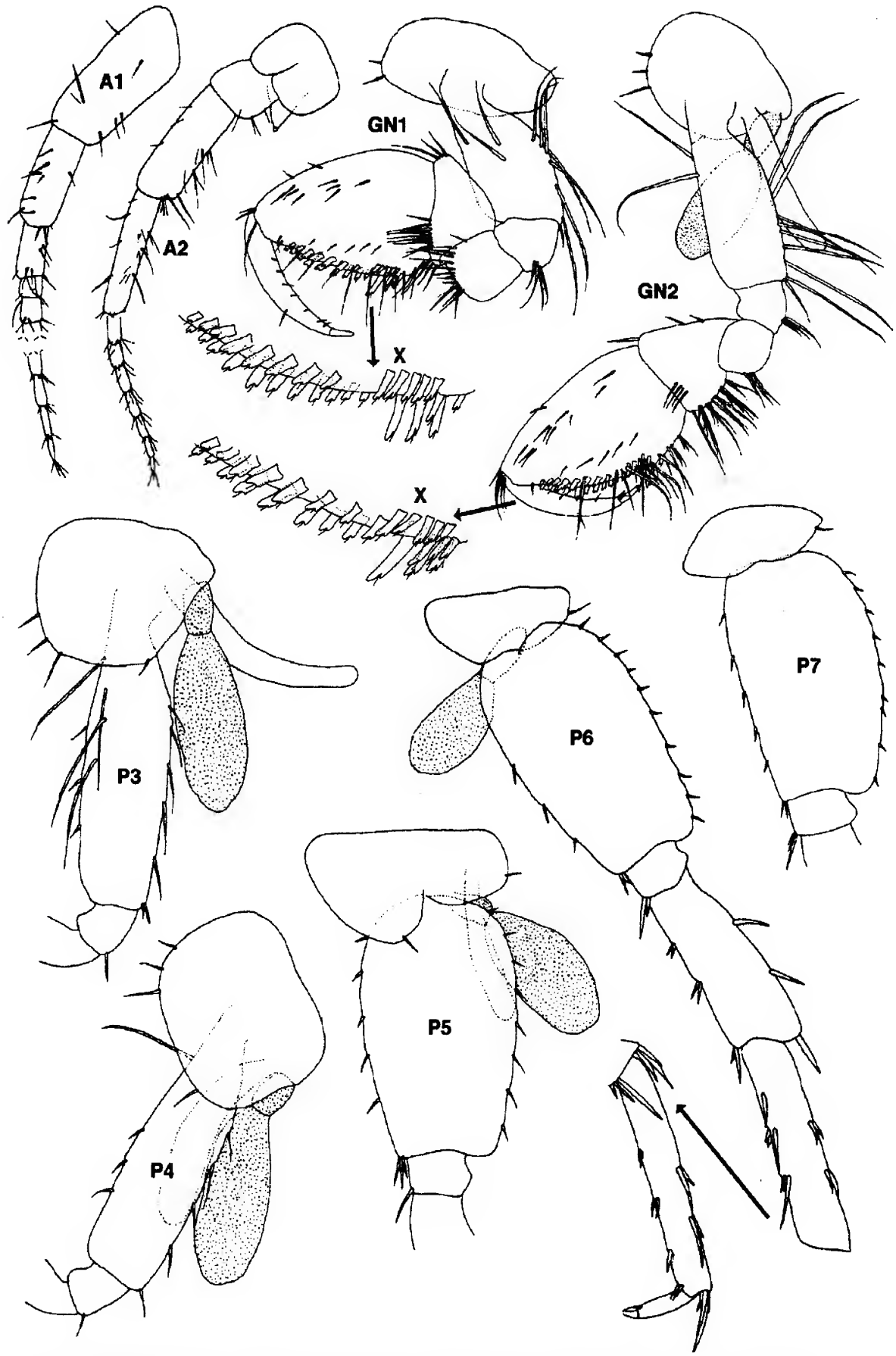

Fig. 2. ***Stygobromus rallus*, n. sp.** Female (7.6 mm). Whitman County, Washington.

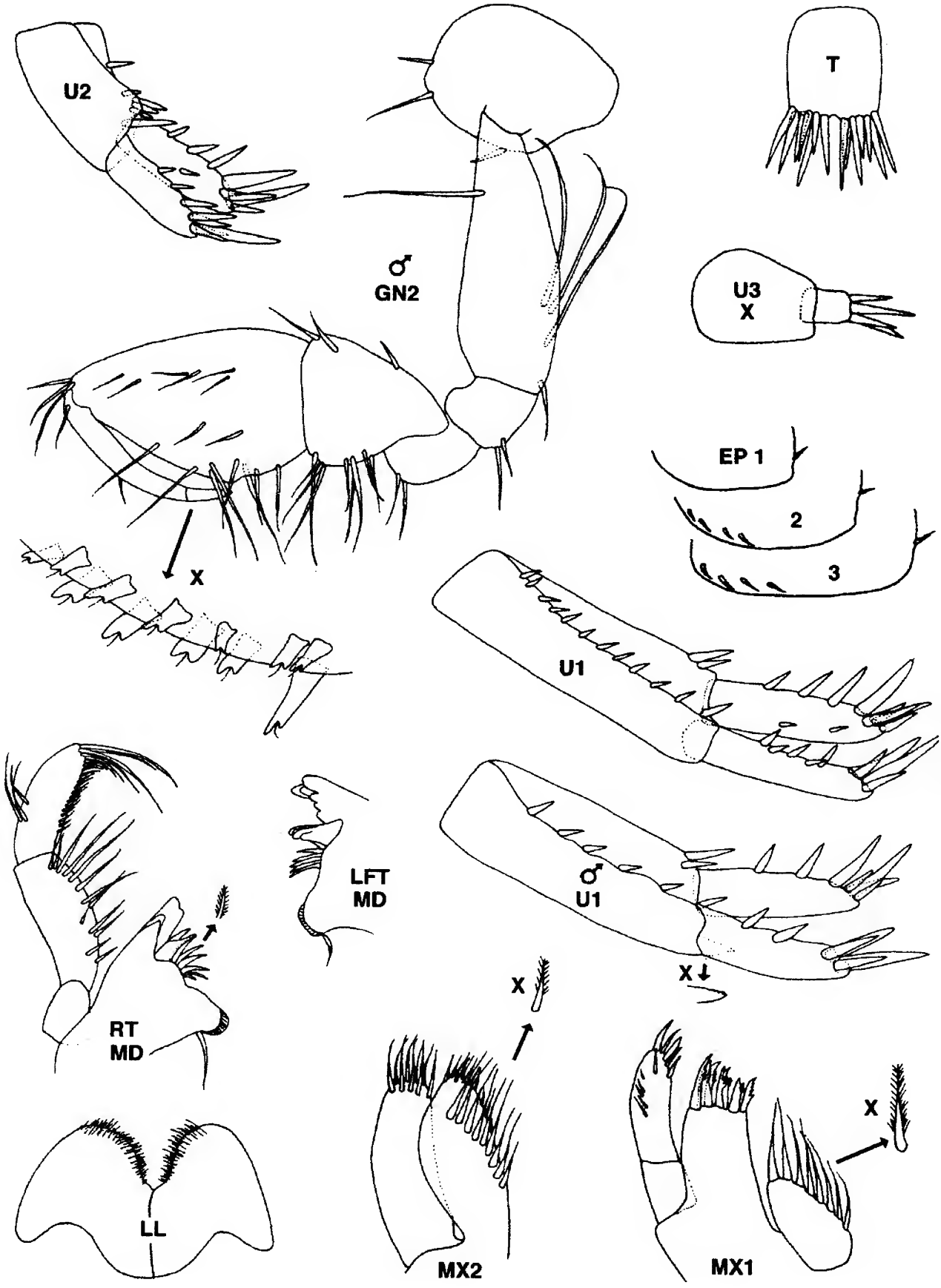

Fig. 3. ***Stygobromus rallus*, n. sp.** Female (7.7 mm); male (4.5 mm). Whitman Co., Washington.

propod of gnathopod 1 with short posterior margin and more teeth on palmar margin; gnathopod 2 with more teeth on palmar margin; bases of pereopods 4-7 more narrow; uropod 3 with more spines on rami; telson lacking notch on apical margin and with longer and stouter spines. Largest ♀, 11.0 mm; largest♂, 10.0 mm.

Female. Antenna 1: 70 percent length of body, 62 percent longer than antenna 2; primary flagellum with 18 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 6 plumose spines; palp segment 2 with row of 13 rather long setae on inner margin; palp segment 3 bearing 3 B setae, 16 D setae, and 4 E setae, lacking both A and C setae. Inner lobes of lower lip vestigial. Maxilla 1: inner plate with 8 apical, plumose setae; palp with 6 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 9 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 11 plumose setae, 5 naked setae apically, and 4 coarse setae on inner margin; outer plate with setae on inner margin and apex, some slightly plumose, and 1 small spine.

Gnathopod 1: propod subequal in size to that of gnathopod 2; palm slightly convex and about five times longer than posterior margin in length, armed with 27 spine teeth in double row; defining angle with 4 spine teeth on outside, 4 shorter ones on inside; posterior margin with row of 4 setae; approximately 8 superior medial setae, mostly triply inserted; 5-6 singly inserted inferior medial setae; dactyl nail rather short; coxa rather narrow and broader than deep, margin with 2 setae. Gnathopod 2: propod palm straight or weakly convex and armed with 29-30 spine teeth in double row; defining angle with 4 spine teeth of unequal length on outside, 2 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 3 sets of mostly triply inserted setae; 10 superior medial setae, mostly triply inserted; 5 singly inserted inferior medial setae; coxa little broader than deep, margin with 3 setae.

Pereopod 3: coxal plate broader than deep, margin with 4 setae. Pereopod 4: coxal plate broader than deep, reaching about 30 percent length of basis, margin with 4 setae. Pereopod 6 little longer than pereopod 7, about 78 percent length of body, 43 percent longer than pereopod 5. Pereopods 5-7: bases narrowing in larger specimens, broader proximally than distally; posterior margins convex; distoposterior lobes distinct (but less so on pereopod 7); anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 about 25 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from segment 7. Brood plates somewhat narrowing distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner, that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners tiny but distinct; ventral margin of plate 2 without spines, that of plates 3 with 3 to 4 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 70 percent length of peduncle, with 9 spines; outer ramus with 9 spines; peduncle with 14 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 8 spines; outer ramus with 8 spines; peduncle with 6 spines. Uropod 3: ramus approximately 45 percent length of peduncle, with 4 apical spines.

Telson little longer than broad, apical margin typically with tiny median notch between spine clusters, bearing 14 - 18 relatively long spines.

Male. Differing from female as follows: Gnathopod propods shorter and narrower, palm of propod 2 longer in relation to posterior margin and with fewer teeth on palmer margin. Uropod 1: peduncular process approximately 25 percent length of outer ramus, narrowing distally, upper margin minutely serrate distally; inner ramus with 7 spines; peduncle with 8 spines. Uropod 2: inner ramus with 9 spines, peduncle with 6 spines. Telson with 14 long apical spines.

Distribution and ecology. In addition to Millers Spring no. 2 and Rock Lake Spring (the type-locality), Mohammad (1995) reported this species from Millers Springs no. 3 and 4, Spokane Co., WA and Dragon Spring, Adams Co., Washington. This species co-occurs with *S. latus* in Rock Lake Spring and Millers Spring No. 2

Etymology. The epithet *rallus* means "thin" or "narrow," in reference to the bases of pereopods 5 - 7, which are relatively narrow in comparison to those of the sympatric *S. latus*.

Remarks: This is the same species that Ibrahim Mohammad named *Stygobromus chrissi* in his unpublished 1995 master's degree thesis at Eastern Washington University.

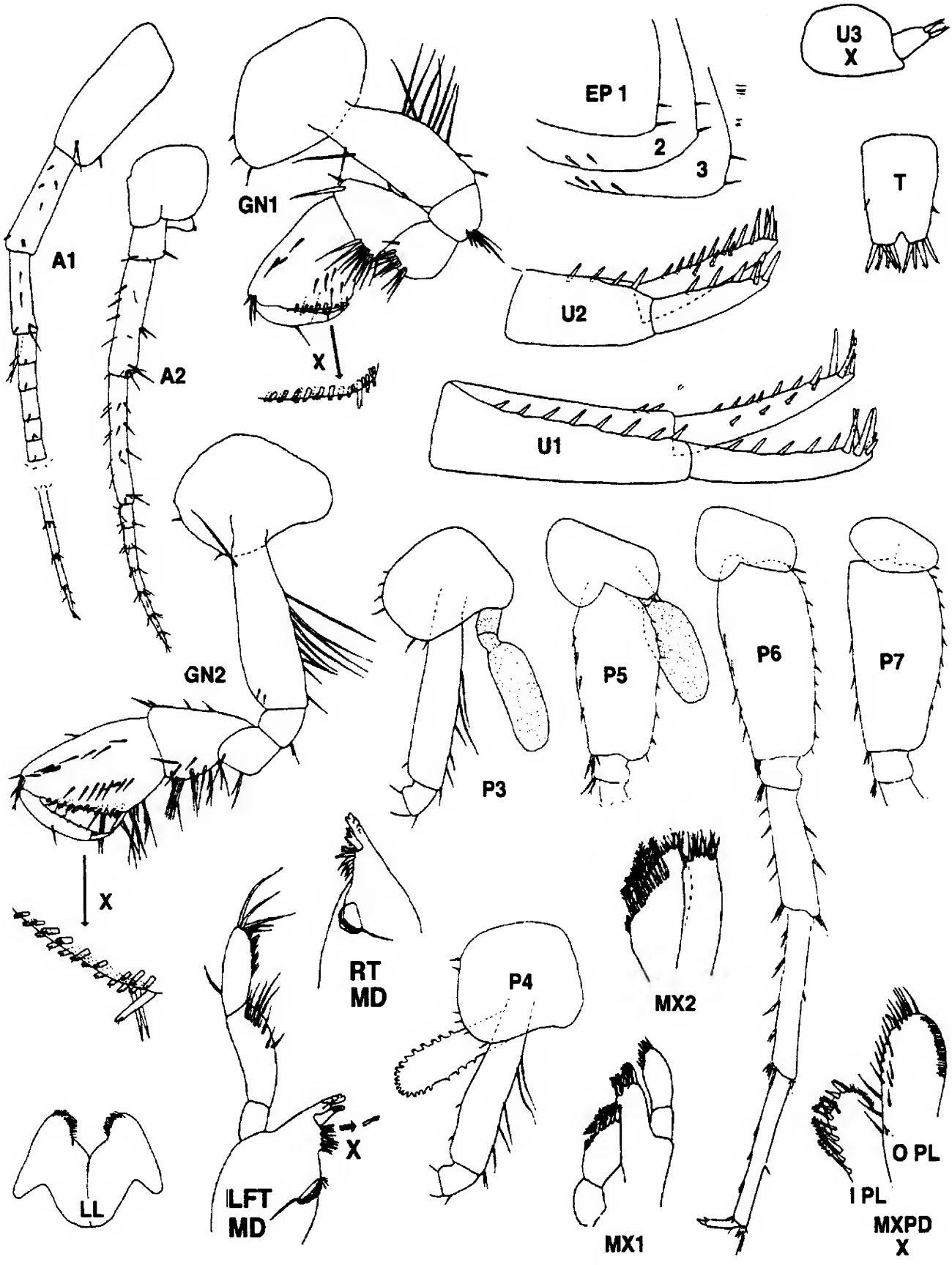

Fig. 4. ***Stygobromus limbus*, n. sp.** Female (10.0 mm). Culberson County, Texas.

Stygobromus limbus, new species
(Fig. 4)

Material examined. TEXAS. Culberson Co.: Border Cave, HOLOTYPE ♀ (on slide mounts in part) (USNM 1000067), W. C. Welbourn, 1 Nov. 1976; 12 ♀♀, paratypes, 16 juvs., S. J. Harden and C. T. Lindblom, 4 July 1985; 8 ♀♀, 1 ♂, S. J. Harden and C. T. Lindblom, 15 Aug. 1986.

Diagnosis. A relatively large cavernicolous species possibly related to *S. azisonensis* in structure of the gnathopods but distinguished from that species as follows: maxillae 1 and 2 with more setae on inner plate; maxilliped with more long setae on inner plate; distoposterior lobe of pereopod 6 better developed; coxal plates 3-4 with more setae on margin; pleonal plates 2-3 with more spines on ventral margin; uropods 1-2 with more spines on rami and peduncle; and telson with shorter apical spines and slight notch. Largest ♀, 12.5 mm; ♂ unknown.

Female. Antenna 1: 50 percent length of body, 45 percent longer than antenna 2; primary flagellum with 19-20 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 6-7 plumose spines; palp segment 2 with row of 8 long setae on inner margin; palp segment 3 bearing 1 B seta, 11 D setae, and 5 setae E, lacking both A and C setae. Inner lobes of lower lip absent. Maxilla 1: inner plate with 11 apical, plumose setae; palp with 8 stiff setae subapically. Maxilla 2: inner plate with oblique row of 13 plumose setae on inner margin. Maxilliped: inner plate with 3-4 bladelike spines, 5 plumose spines, 1 naked seta apically, and 5 plumose setae on inner margin; outer plate with setae on inner margin and apex, and single small spine near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight and approximately 2 times longer than length of posterior margin, armed with 20 spine teeth in double row; defining angle with 2 spine teeth on outside, 4 shorter ones on inside; posterior margin lacking setae; 2-3 superior medial setae; 2-3 inferior medial setae; dactyl nail rather long; coxa broader than deep, margin with 3 setae. Gnathopod 2: propod subrectangular, deeper than broad; palm straight or slightly concave and armed with 20 spine teeth in double row; defining angle with 1 spine tooth on outside, 1 shorter spine tooth on inside; posterior margin 50 percent as long as palm, with 2 sets of doubly inserted setae; 10 superior medial setae, triple inserted; 5 inferior medial setae; coxa deeper than broad, margin with 3 setae.

Pereopod 3: coxal plate deeper than broad, margin with 6 setae. Pereopod 4: coxal plate relatively broad, reaching about 35 percent length of basis, margin with 6 setae. Pereopod 6 little longer than pereopod 7, about 55 percent length of body, 30 percent longer than pereopod 5. Pereopods 5-7: bases little broader proximally than the distally; posterior margins weakly convex; distoposterior lobes poorly developed; anterior margin with 3-5 spines, posterior margins with numerous spines; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 approximately 20 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates little expanded distally.

Pleonal plates: posterior margin of plate 3 convex, with 2 setules near distoposterior corner, that of 1 and 2 less convex, each also with 2 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral superior margin of plate 2 with 2 spines, that of plate 3 with 3 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 75 percent length of peduncle, with 15 spines; outer ramus with 11 spines; peduncle with 10 spines. Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 16 spines; outer ramus with 6 spines; peduncle with 5 spines. Uropod 3: peduncle usually without small setae; ramus approximately 50 percent length of peduncle, with 2 apical spines.

Telson little longer than broad, tapered distally; apical margin with small notch between spine clusters, bearing 8-9 relatively long spines.

Distribution and ecology. This species is known only from its type-locality, a cave developed in gypsum bedrock, where it has been collected on several occasions from phreatic lakes on the cave's lower level. Samples were collected from rocks in deep lakes with the stygobiont isopod *Lirceolus nidulus* Lewis (see Lewis 2001). All of the females collected by Harden and Lindblom in the summer of 1985/86 were ovigerous.

Etymology. This species is named for the type-locality, Border Cave. The epithet *limbus* is from the Latin, meaning "border".

Stygobromus fontinalis, new species
(Figs. 5, 6)

Stygobromus sp. B: — Ward and Holsinger, 1981: 64-67.

Material examined. COLORADO. Rio Blanco Co.: spring, ca. 32 km northwest of Rio Blanco, HOLOTYPE ♀ (USNM 1000056), 2 ♂♂ and 1 ♀ paratypes, J. V. Ward, 19 May 1977; 5 ♂♂, 5 ♀♀, J. V. Ward, 20 May 1977; spring at mouth of Stewart Gulch, ca. 32 km north-northwest of Rio Blanco, 1 ♀, J. V. Ward, 2 Nov. 1979.

Diagnosis. A medium-sized groundwater species, closely related to *S. holsingeri* in gnathopods and uropods 1-2, but distinguished from that species as follows: maxilliped with 3 bladelike apical spines on inner plate; gnathopods with more teeth on palmar margin of propods; palmar margin of gnathopod 1 straight or slightly convex; maxillae 1 and 2 with more setae on inner plate; telson proportionately longer. Largest ♀, 7.5 mm; largest ♂, 6.5 mm.

Female. Antenna 1: 60 percent length of body, 57 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 6 plumose spines; palp segment 2 with row of 8 rather long setae on inner margin; palp segment 3 bearing 1 B seta, 13 D setae, 3 E setae, lacking both A and C setae. Inner lobes of lower lip vestigial. Maxilla 1: inner plate with 9 apical, plumose setae; palp with 8 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 10 plumose setae on inner margin. Maxilliped: inner plate with 3 bladelike spines, 5 plumose spines, 2 naked setae apically, and 4 plumose setae on inner margin; outer plate with setae on inner margin and face, and on or near apex.

Gnathopod 1: propod shorter than that of gnathopod 2; palm slightly convex and about 30 percent longer than posterior margin in length, armed with 27-28 spine teeth in double row; defining angle with 3 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; 2 superior medial setae; about 6 singly inserted inferior medial setae; dactyl nail rather short; coxa much broader than deep, margin with 3 setae. Gnathopod 2: propod longer than broad; palm straight or slightly concave and armed with 21 spine teeth in double row; defining angle with 1 long spine tooth on outside, 3 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 1 cluster of setae; 9 superior medial setae, most doubly inserted; about 4 singly inserted inferior medial setae; coxa broader than deep, margin with 2 setae.

Pereopod 3: coxal plate deep, about as broad as deep, margin with 2 setae. Pereopod 4: coxal plate relatively broad and deep, reaching about 30 percent length of basis, margin with 6 setae. Pereopod 6 little longer than pereopod 7, about 67 percent length of body, 50 percent longer than pereopod 5. Pereopods 5-7: bases of about as broad proximally as distally; posterior margins convex; distoposterior lobes developed but not prominent; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 about 25 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates slightly narrowing distally.

Pleonal plates: posterior margin of plate 1 with 1 setule near distoposterior corner, those of 2 and 3 weakly convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 4 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 67 percent length of peduncle, with 8 spines; outer ramus with 8 spines; peduncle with 11 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, heavily spined, with 19 spines, many toward distal end; outer ramus with 6 spines; peduncle with 4 spines. Uropod 3: peduncle without setae; ramus approximately 33 percent length of peduncle, with 3 apical spines.

Telson little longer than broad, gently tapered distally; apex with tiny median notch between spine clusters, bearing 11-12 relatively long spines.

Male. Differing from female as follows: Gnathopod propods broader, palm of propod 2 with more teeth on margin. Uropod 1: peduncular process 20 percent length of outer ramus, sharply pointed distally, upper margin minutely serrate; inner ramus with 8 spines; peduncle with 6 spines. Uropod 2: inner ramus with 24 spines, peduncle with 4 spines. Telson with 12 apical spines.

Distribution and ecology. The species is recorded from its type-locality and a spring at the mouth of Stewart Gulch, both in Rio Blanco County, Colorado. The salinity of the type-locality springs was about 1,000 mg/L at the time of collection, 19 and 20 May, 1977 (Ward and Holsinger 1981).

Etymology. The epithet *fontinalis* is from the Latin,

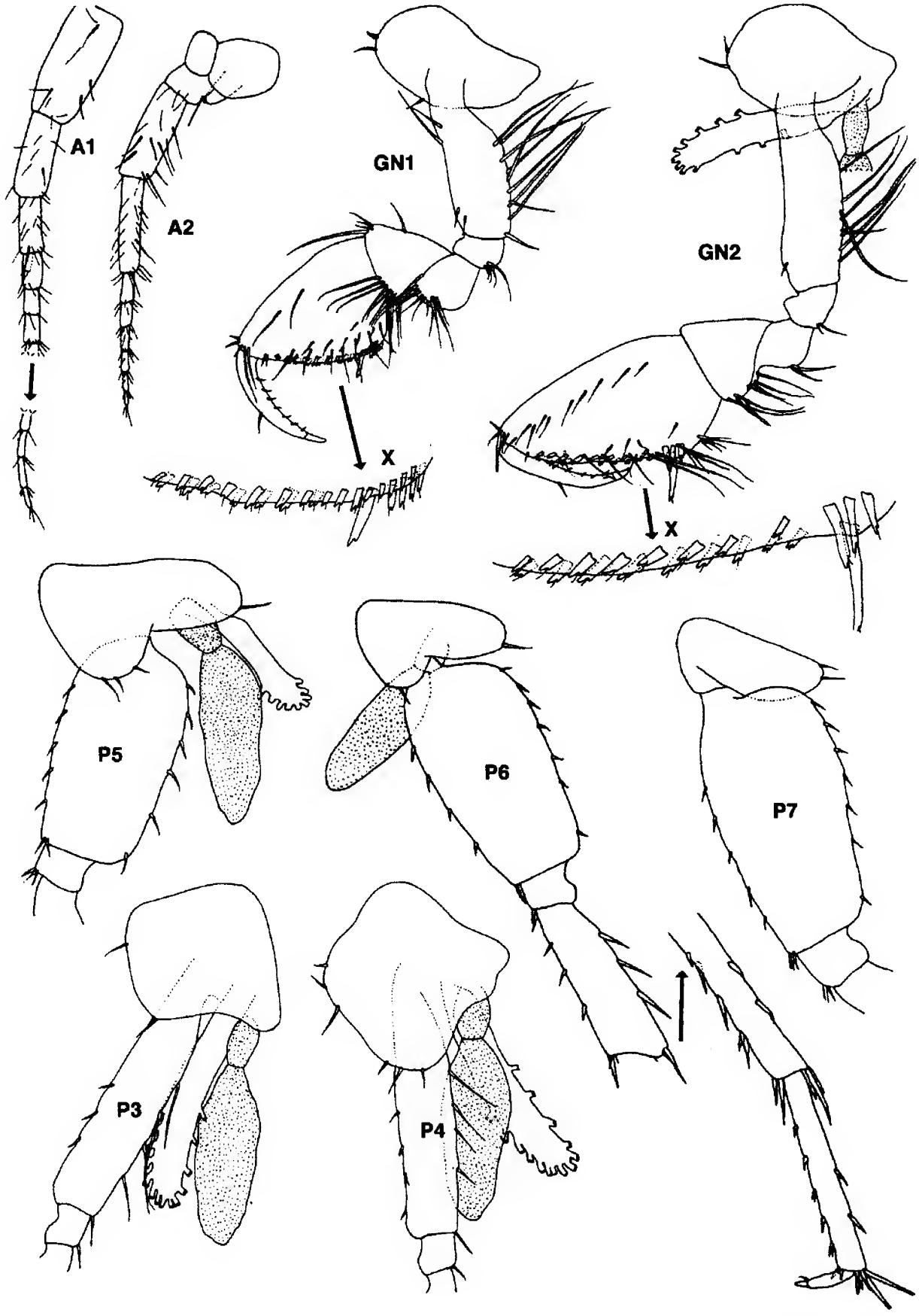

Fig. 5. ***Stygobromus fontinalis*, n. sp.** Female (7.5 mm). Rio Blanco County, Colorado.

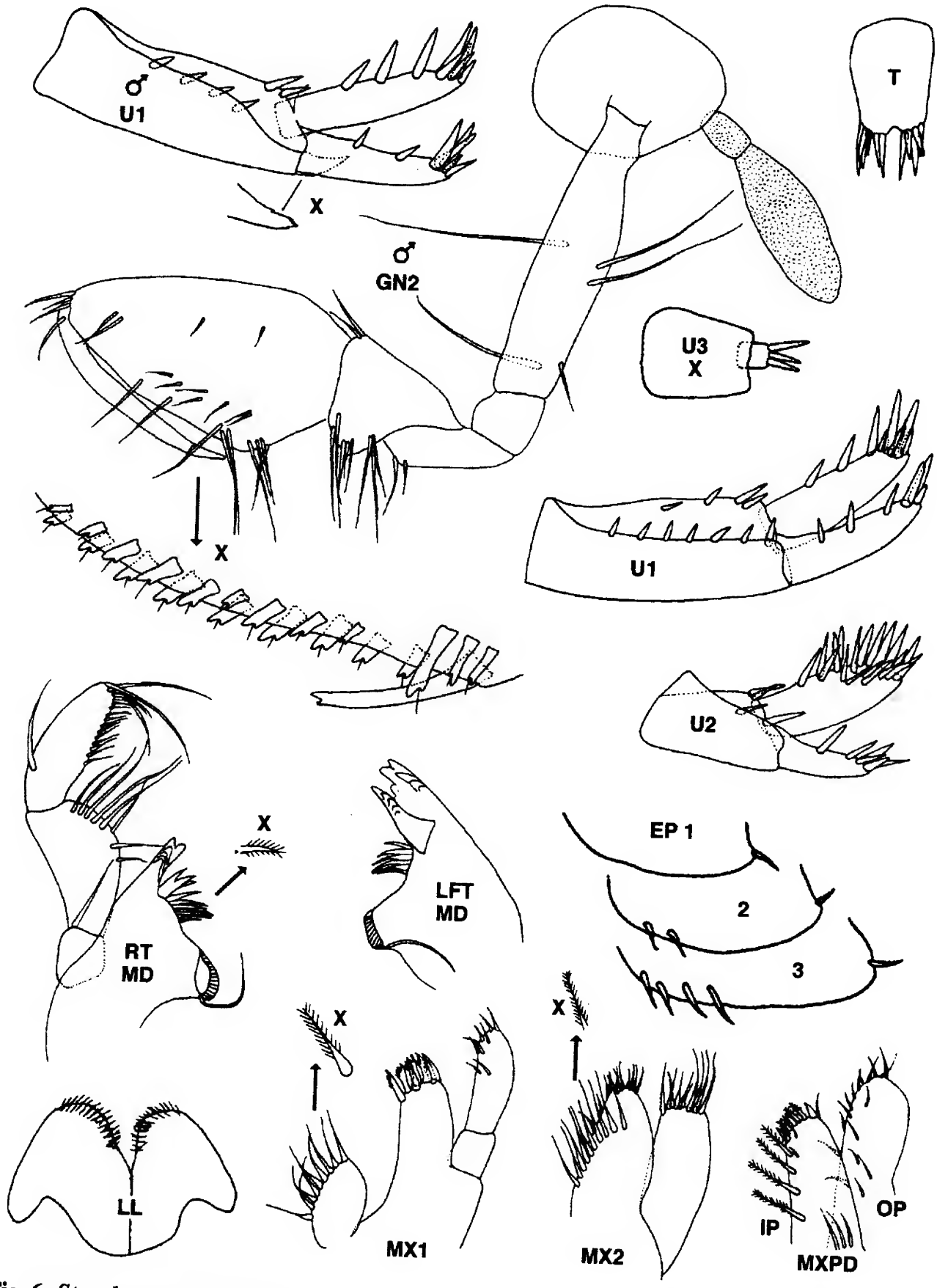

Fig. 6. ***Stygobromus fontinalis*****, n. sp.** Female (7.5 mm); male (6.0 mm). Rio Blanco Co.,Colorado.

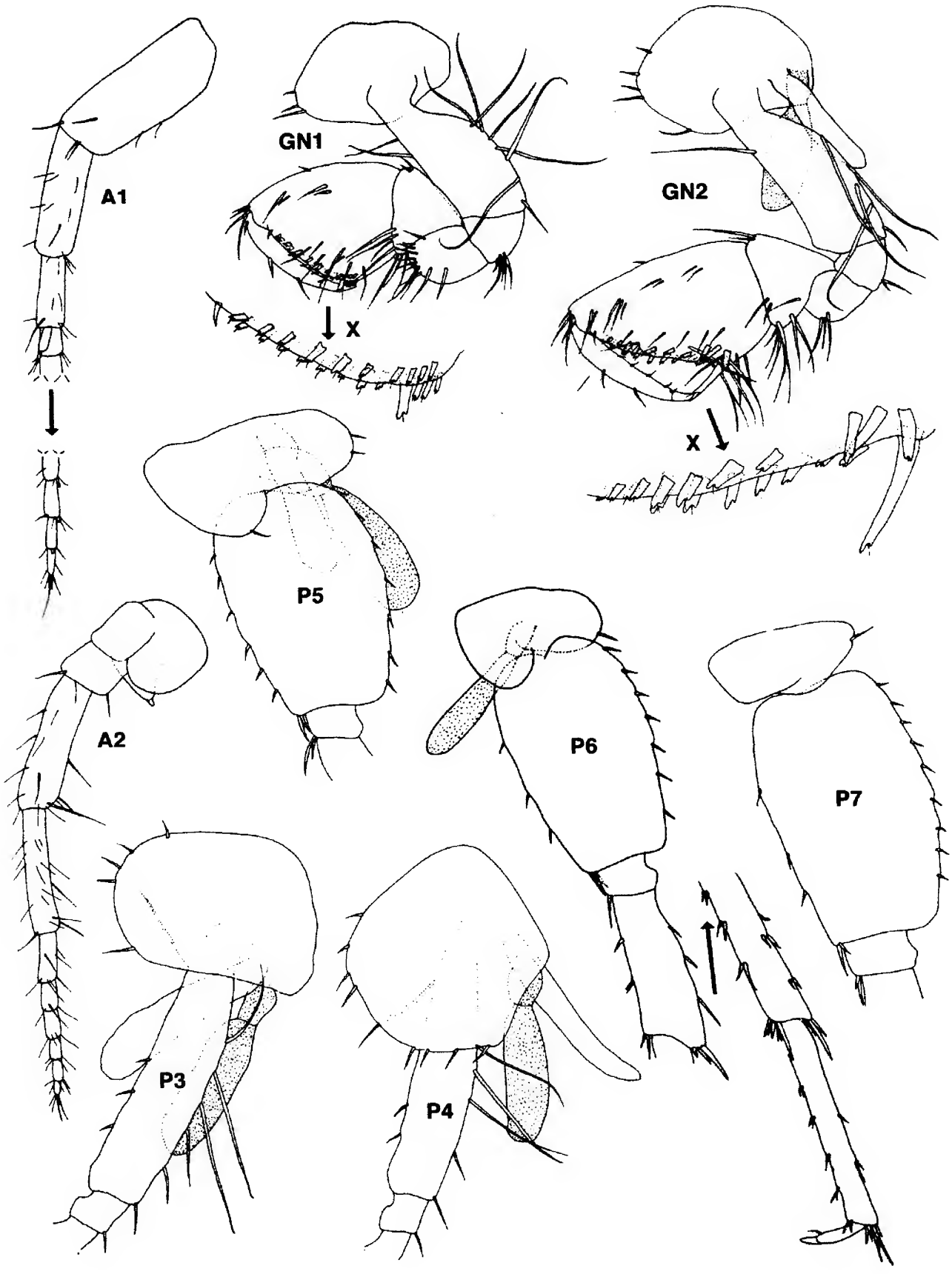

Fig. 7. ***Stygobromus jemezensis*, n. sp.** Female (6.5 mm). Sandoval County, New Mexico.

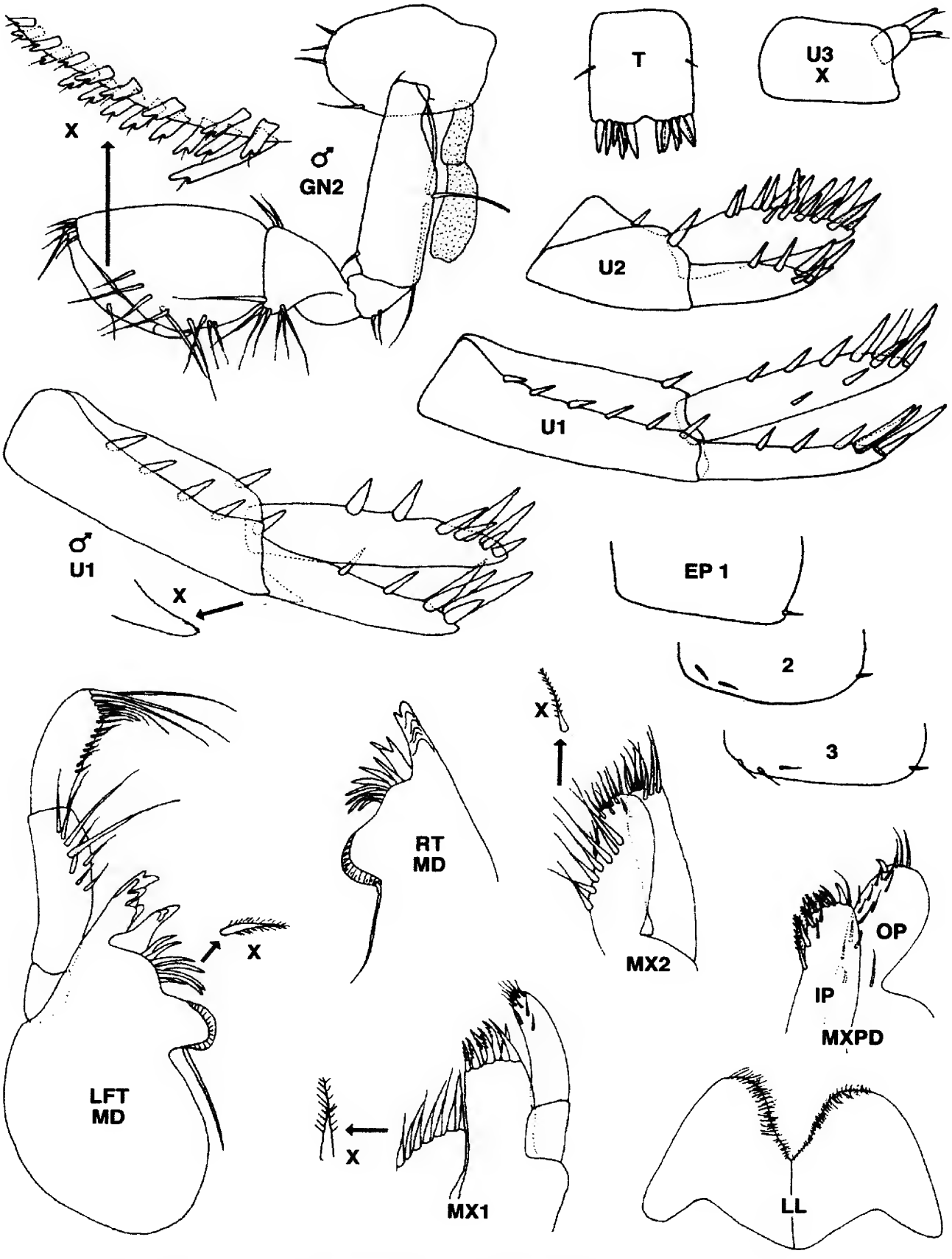

Fig. 8. ***Stygobromus jemezensis*****, n. sp.** Female (6.5 mm); male (4.2 mm).
Sandoval Co., New Mexico

meaning "a spring," with refererence to the spring habitat of the species.

Stygobromus jemezensis, new species
(Figs. 7, 8)

Material examined. NEW MEXICO. Sandoval Co.: unnamedwell at Bland, HOLOTYPE ♀ (USNM 1000064), 1 ♀ and 1 ♂ paratypes (MSB), B. Wilson, 29 Aug. 1994.

Diagnosis. A medium-sized groundwater species, closely related to *S. arizonensis* in structure of gnathopods but distinguished from that species as follows: propod of gnathopod 1 with more teeth on palmar margin; pereopod 6 with distinct distoposterior lobe; posterior margins of pleonal plates with 1 setule; uropod 1-2 with more spines on rami (similar to *S. holsingeri*); uropod 3 with proportionately broad peduncle; telson with short spines and slight apical notch. Largest ♀, 7.0 mm; largest ♂ 4.5 mm.

Female. Antenna 1: 52 percent length of body, 57 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 7 plumose spines; palp segment 2 with row of 8 rather long setae on inner margin; palp segment 3 with 10 D and 5 E setae, lacking A, B and C setae. Inner lobes of lower lip absent. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 10 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 7 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 3 plumose spines, 2 naked setae on or near apical margin, 3 plumose setae on inner margin; outer plate with numerous short setae on inner margin and 1 bladelike spine and several setae on or near apex.

Gnathopod 1: propod slightly shorter than propod of gnathopod 2; palm straight or slightly concave, about half length of posterior margin, armed with 22 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin without setae; superior medial setae 4, doubly inserted; 2-5 inferior medial setae; dactyl nail rather long; coxa deeper than broad, margin with 3 setae. Gnathopod 2: propod subrectangular, longer than broad; palm armed with 19-20 spine teeth in double row; defining angle with 1 very long spine tooth on outside, 1 shorter spine tooth on inside; posterior margin about 33 percent length of palm, with 2 setae; 9 superior medial setae, doubly or triply inserted; 5 or 6 singly inserted inferior medial setae; coxa deeper than broad, margin with 5 setae.

Pereopod 3: coxal plate deeper than broad, margin with 5 long setae. Pereopod 4: coxal plate relatively broad and deep, reaching about 45 percent length of basis, margin with 8 setae. Pereopod 6 little longer than pereopod 7, about 66 percent length of body, 30 percent longer than pereopod 5. Pereopods 5-7: bases little broader proximally than distally; posterior margins convex; distoposterior lobes distinct but not prominent; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 typically 33 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates narrowing distally.

Pleonal plates: posterior margins of plate 1 and 3 convex, each with 1 setule near distoposterior corner, that of 2 less convex, with 1 setule near distoposterior corner; distoposterior corners rounded and distinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 3 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 90 percent length of peduncle, with 10 spines; outer ramus with 7 spines; peduncle with 7 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 17 relatively long spines; outer ramus with 7 long spines; peduncle with 2 spines. Uropod 3: peduncle without setae or spines; ramus approximately 30 percent length of peduncle, with 2 apical spines.

Telson little longer than broad; apical margin with tiny median notch between spine clusters, bearing 12 relatively short spines.

Male. Differing from female as follows: gnathopod propods smaller, palm of propod 2 longer in relation to posterior margin and with more teeth on palmar margin. Uropod 1: peduncular process present and reaching about 25 percent length of outer ramus, bluntly rounded distally, upper margin slightly serrate; inner ramus with 8 spines; peduncle with 6 spines. Uropod 2: inner ramus with 16 spines, peduncle with 3-4 spines. Telson with 15 short apical spines.

Distribution and ecology. The species is known from its type-locality, where it was collected from a deep water well in the Jemez Mountains of New Mexico.

Etymology. The species is named for the location of the type-locality in the Jemez Mountains.

Stygobromus herbsti, new species
(Figs. 9, 10)

Material examined. NEVADA. Elko Co.: Ruby Lake National Wildlife Refuge, spring No. 121, HOLOTYPE ♀ (USNM 1000059), 9 ♂♂ and 6 ♀♀ paratypes (2 partly on slide mounts), D. B. Herbst, 10 June 1997; spring No. 229, 2 ♀♀, D. B. Herbst, 10 June 1997; spring No. 129, 13 ♂♂, 5 ♀♀, 1 juv., D. B. Herbst, 9 June 1997, spring No.103, 5 ♀♀, 1 ♂, D. B. Herbst, summer 1997; White Pine Co.: Ruby Lake National Wildlife Refuge, spring No. 208, 1 ♂, 18 juvs, D. B. Herbst, 14 Sept. 1997; spring No. 191, 4 ♂♂, 17 ♀♀, 16 juvs., D. B. Herbst, 13 Sept. 1997, spring No. 180, 4 ♂♂, 15 ♀♀, 12 juvs, D. B. Herbst, 12 Sept. 1997; spring No. 223, 5 ♂♂, 2 ♀♀, 9 juvs, D. B. Herbst, 14 Sept. 1997; spring No. 217, 22 juvs, D. B. Herbst, 14 Sept. 1997; spring No. 219, 3 ♂♂, 1 ♀, 26 juvs, D. B. Herbst, 14 Sept. 1997.

Diagnosis. A medium-sized species, closely similar to *S. grahami* and *S. gradyi*, but distinguished from those 2 species as follows: maxilla 1 and maxilliped with fewer setae on inner plate; palms of gnathopod 1 and 2 with more spines; coxal plate of gnathopod 2 broader than deep; lacking distoposterior lobes of pereopod 6 or poorly developed; pleonal plate 2 with fewer ventral spines; uropod 3 with relatively longer peduncle; and telson apical margin with very tiny notch. Largest ♀, 8.5 mm; largest ♂ 6.0 mm.

Female. Antenna 1: 50 percent length of body, 30 percent longer than antenna 2; primary flagellum with 17 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 6-7 plumose spines; palp segment 2 with 10 rather long setae on inner margin; palp segment 3 with 12 D setae, 6 E setae, lacking A, B and C setae. Inner lobes of lower lip small to vestigial. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 10 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 12 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 3 plumose spines, 3 naked setae apically and 2 plumose spines on inner margin; outer plate with setae on inner margin and apex and 5 or 6 small serrate spines on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight or slightly convex and about 60 percent longer than posterior margin, armed with 24 spine teeth in double row; defining angle with 3 apine teeth on outside, 2 shorter ones on inside; posterior margin with 2 setae; 3 superior medial setae; 10 inferior medial setae; dactyl nail long; coxa about 33 percent deeper than broad, margin with 4 setae. Gnathopod 2: propod little longer than broad, palm straight or slightly concave medially and armed with 26 spine teeth in double row; defining angle with 1 long spine tooth on outside, 3 shorter spine teeth on inside; posterior margin approximately 50 percent length of palm, with row of setae; 14 mostly double-inserted superior medial setae; about 12 singly inserted inferior medial setae; coxa broader than deep, margin with 10 setae.

Pereopod 3: coxal plate deeper than broad, margin with 8 setae. Pereopod 4: coxal plate relatively broad and deep, about as deep as broad, reaching about 33 percent length of basis, margin with 11 setae. Pereopod 6 little longer than pereopod 7, about 53 percent length of body, 13 percent longer than pereopod 5. Pereopods 5-7: bases rather narrow, broader proximally than distally; posterior margins slightly convex, disto-posterior lobes indistinct; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 typically 30 percent length of corresponding propod. Coxal gills present on pereopods 2-6. Brood plates little expanded distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner, that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded; ventral margin of plates 2 and 3 with 4 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 65 percent length of peduncle, with 12 spines; outer ramus with 7 spines; peduncle with 13 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 11 spines; outer ramus with 5 spines; peduncle with 5 spines. Uropod 3: peduncle usually bearing 2 small setae; ramus approximately 30 percent length of peduncle, with 4 apical spines.

Telson little longer than broad, apical margin entire or with tiny median notch between spine clusters, usually bearing 12 spines, some relatively long.

Male. Differing from female as follows: Gnathopod propods narrow; palm of propod 2 shorter in comparison with posterior margin. Uropod 1: peduncular process approximately 33 percent length of outer ramus, bluntly rounded distally, lower margin minutely serrate; inner ramus with 8 -9 spines; peduncle with 7-8 spines. Uropod 2: inner ramus with 12-14 spines, peduncle with 10-13 spines. Telson with 10-12 apical spines.

Distribution and ecology. This species is recorded from a series of springs in the Ruby Lake National Wildlife Refuge, Elko and White Pine Cos., Nevada.

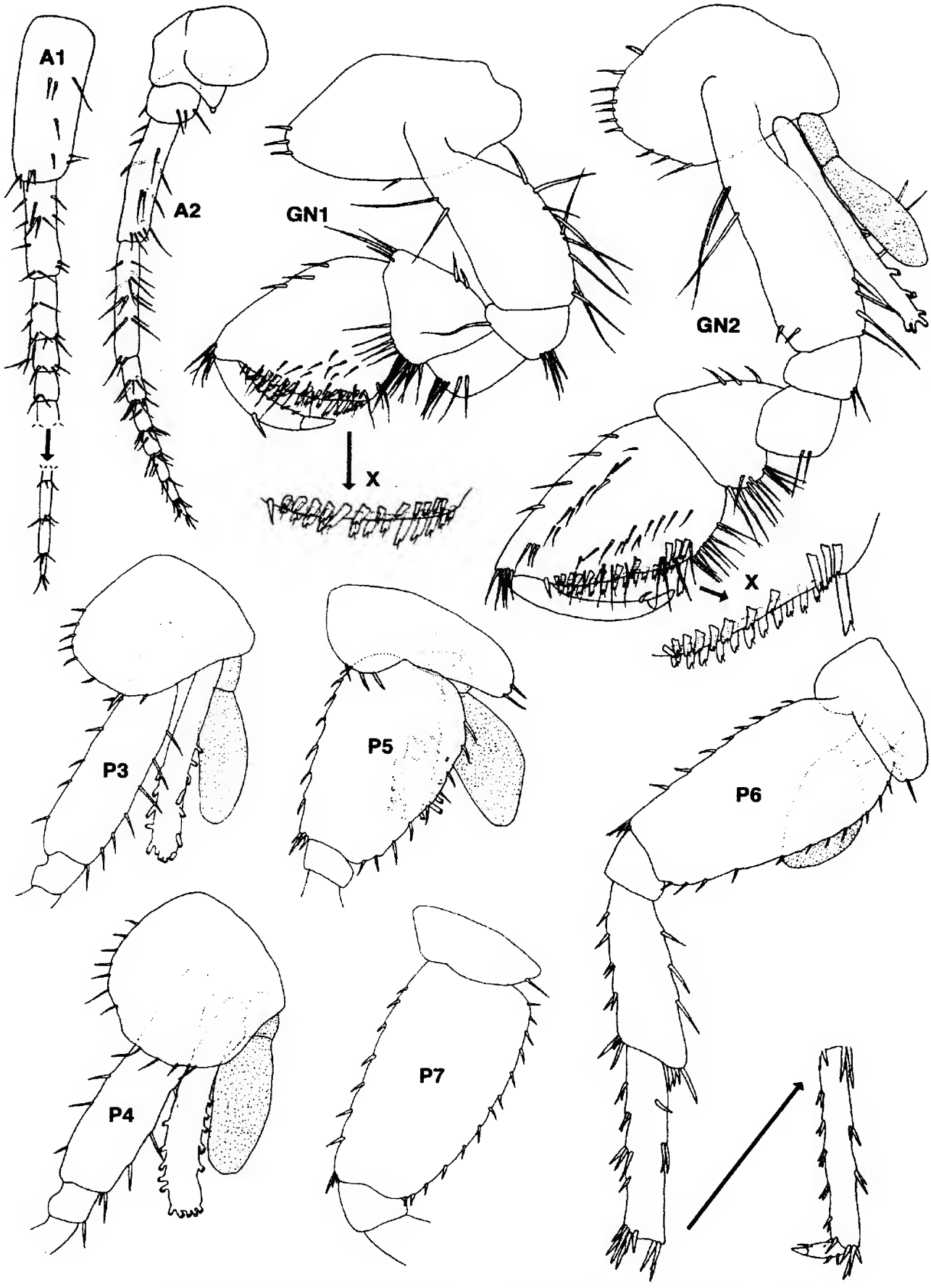

Fig. 9. ***Stygobromus herbsti,*** **n. sp.** Female (8.5 mm). Elko County, Nevada.

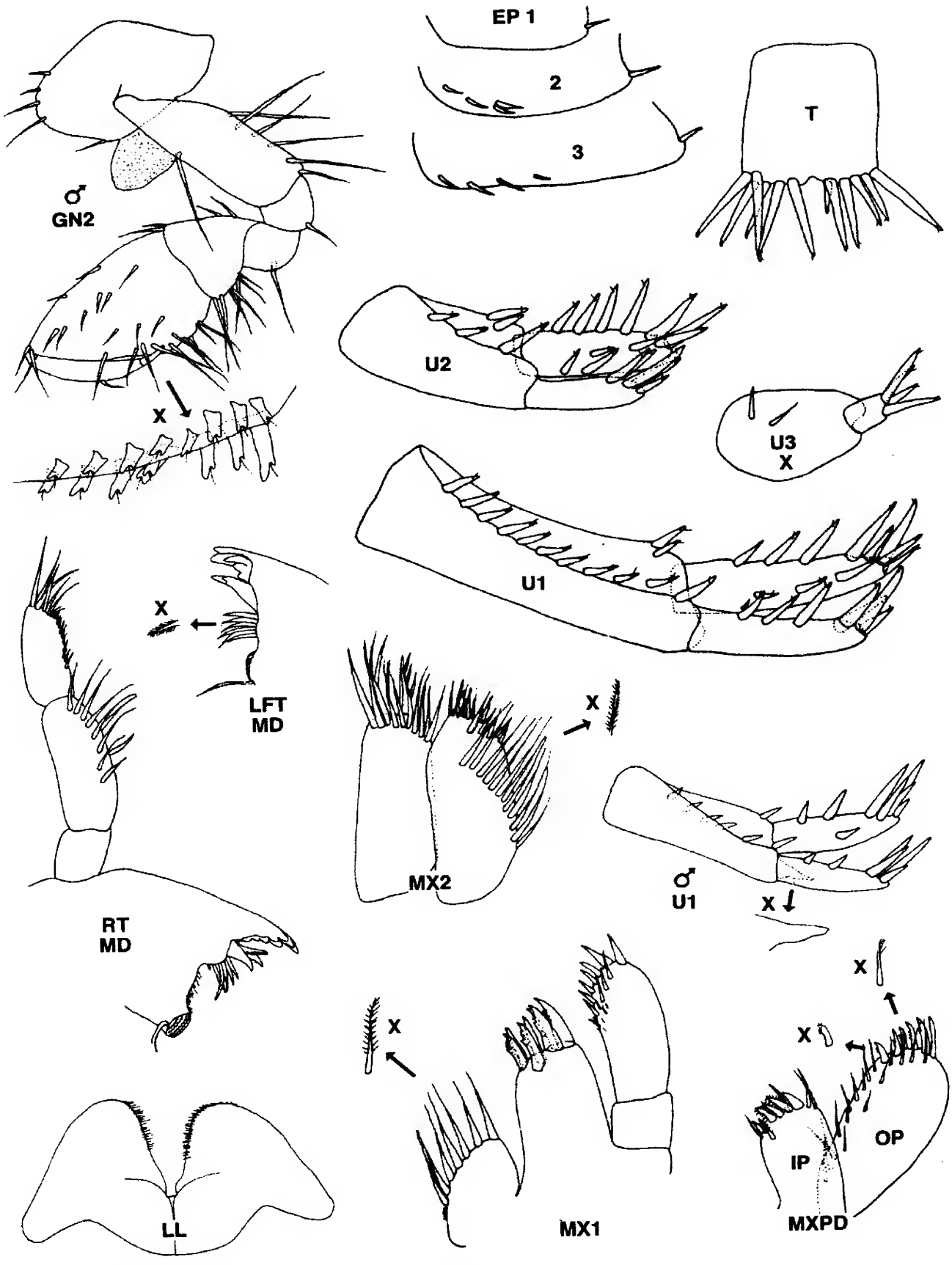

Fig.10. ***Stygobromus herbsti*****, n. sp.** Female (8.5 mm); male (5.5 mm). Elko County, Nevada.

Etymology. The species is named in honor of its collector, Dr. David B. Herbst.

Stygobromus trinus, new species
(Figs. 11, 12)

Material examined. CALIFORNIA. Trinity Co.: Hall City Cave, about 54.4 km W. of Redding. HOLOTYPE ♀ (USNM 1000072), ♀ paratypes, D. C. Rudolph, B. Martin and S. Winterath, 11 Apr. 1979.

Diagnosis. A medium-sized cavernicolous species, closely similar to *S. grahami* but distinguished as follows: maxilla 2 with fewer setae on inner plate; palms of gnathopods 1 and 2 straight; coxal plate of pereopod 3 broader than deep; pleonal plates 1 and 2 with more ventral spines; uropod 3 with tiny ramus; and apical margin of telson with very shallow notch. Size of largest ♀ 7.0 mm, ♂ unknown.

Female. Antenna 1: 60 percent length of body, 80 percent longer than antenna 2; primary flagellum with 18 segments. Antenna 2: flagellum with 7 segments.

Mandibles: spine row with 6 plumose spines; palp segment 2 with 8 long setae on the inner side; palp segment 3 with 10-11 C setae, few D setae, 3 E setae, lacking A and B setae. Inner lobes of lower lip vestigial or absent. Maxilla 1: inner plate with 9 apical, plumose setae; palp with 6 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 10 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 3 plumose spine, 2 naked setae apically, and 3 plumose setae on inner margin and apex; outer plate with 1 bladelike spine and 5 or 6 small serrate pines on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight and about 50 percent longer than posterior margin, armed with 22 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin lacking setae; 4 superior medial setae; 4 -5 inferior medial setae, all singly inserted; dactyl nail short; coxa approximately 2 times deeper than broad, margin with 4 setae. Gnathopod 2: propod subrectangular, longer than broad; palm sinuate (concave medially) and armed with 23 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2-3 shorter spine teeth on inside; posterior margin about 33 percent length of palm, with 2 sets of triply inserted setae; 8 doubly inserted superior medial setae; 4 inferior medial setae, singly inserted; coxa deeper than broad, margin with 4 setae.

Pereopod 3: coxal plate about as broad as deep, margin with 5-6 setae. Pereopod 4: coxal plate broader than deep, reaching about 40 percent length of basis, margin with 5 setae. Pereopod 6, slightly longer than pereopod 7, about 60 percent length of body, 33 percent longer than pereopod 5. Pereopods 5-7: bases as broad or slightly broader proximally; posterior margins nearly straight; distoposterior lobes distinct but not well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with variable spines; dactyls of pereopods 5-7 not elongate, that of pereopod 6 about 30 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from pereopod 7. Brood plates narrowing distally.

Pleonal plates: posterior margin of plates 2 and 3 slightly convex, with 1 seta each near distoposterior corner, that of 1 less convex, with 1 setule near distoposterior corners; distoposterior corner rounded and indistinct, ventral margin of plate 1 with 4 spines; ventral margin of plate 2 with 3 spines, that of plate 3 also with 4 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 9 spines; outer ramus with 8 spines; peduncle with 8 spines. Uropod 2: inner ramus longer than outer ramus, longer than peduncle, with 12 spines; outer ramus with 6 spines; peduncle with 2 spines. Uropod 3: peduncle without setae; ramus approximately 25 percent length of peduncle, with 3-4 apical spines.

Telson longer than broad, subrectangular; apical margin with tiny median notch between spine clusters, bearing 10-12 relatively long spines.

Distribution and ecology. This species is known only from its type-locality, Hall City Cave, where it was collected from wood debris near the edge of a deep pool (D. C. Rudolph, pers. comm.).

Etymology. The epithet *trinus* is from the Latin, which is based on the geographic place name, Trinity County.

Stygobromus tritus Holsinger, 1974

Stygobromus tritus Holsinger, 1974: 8-11, figs. 2-3 [type-locality: well at Victor Crossing, Ravalli Co., Montana].

Material examined. MONTANA. Missoula Co.: shallow water wells (2.6-6.6 m depth) in Missoula, 14 ♀♀, 4 ♂♂, 1 juv., M. E. Ver Hey, May 1986.

Diagnosis. A rather small subterranean species distin-

guished by the diagnosis and description of Holsinger (1974). Largest ♀, 5.0 mm; largest ♂, 4.5 mm.

Distribution and ecology. This species is recorded from a well at Victor Crossing, Ravalli Co. Montana (see Holsinger 1974) and wells in Missoula County (see above). Females ranging in length from 4.5 to 5.0 mm have setose brood plates and are sexually mature.

Taxonomic remarks: Re-examination of male specimens revealed an apically serrate peduncular process on uropod 1, which was not described in the original description by Holsinger (1974).

Stygobromus boultoni, new species
(Fig. 13)

Material examined. ARIZONA. Maricopa Co.: PVC well no. 1 at Sycamore Creek, about 32 km NE Phoenix, HOLOTYPE ♀ (USNM 1000051), 4 ♀♀ paratypes, 3 juvs., A. Boulton, 12 Mar, 1990; PVC well no. 1, 2 juvs., A. Boulton, 2 Mar, 1990; PVC well no. 3 on Sycamore Creek, 1 ♀, A. Boulton, 2 Mar, 1990.

Diagnosis. A small-sized goundwater species, very similar to *S. arizonensis* but distinguished as follows: palms of gnathopod 1 and 2 oblique and with fewer teeth; maxilla 2 with fewer setae; posterior margin of gnathopods 1 and 2 longer; coxal plates 3 deeper; bases of pereopods 6 and 7 more narrow and with fewer spines on posterior margin; telson with longer apical spines; uropods 1-2 with more long and thick spines on rami; pleonal plates 2 and 3 with more spines on posterior margin. Largest ♀ 4.0 mm, ♂ unkown.

Female. Antenna 1: 54 percent length of body, 43 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 4-5 plumose spines; palp segment 2 with row of 3 rather long setae on inner margin; palp segment 3 with 4 C setae, 5 E setae, lacking A, B and D setae. Inner lobes of lower lip vestigial. Maxilla 1: inner plate with 4 apical, plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 4 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 2 plumose spines, and 3 naked setae apically, and without plumose spines on inner margin; outer plate with 3 setae on inner margin and 4 setae on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight or slightly concave and 2 times longer than posterior margin, armed with 11 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; fewer superior medial setae; lacking inferior medial, dactyl, nail long; coxa broader than deep; margin with 2 setae. Gnathopod 2: propod subrectangular, deeper than broad; palm armed with 9 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin 50 percent of palm in length, with 1 set of setae; 3 superior medial setae, singly inserted; few inferior medial setae; coxa broader than deep, margin with 2 or 3 setae.

Pereopod 3: coxal plate about as broad as deep, margin with 3 setae. Pereopod 4: coxal plate about as broad as deep, reaching about 30 percent length of basis, margin with 2 setae. Pereopod 6 little longer than pereopod 7, about 70 percent length of body, 30 percent longer than pereopod 5. Pereopods 5-7: bases little broader proximally than distally; posterior margins nearly straight; distoposterior lobes not developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 typically 25 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates little narrowing distally.

Pleonal plates: posterior margin of plate 1 and 2 convex, each with 3 spines near distoposterior corner, that of 3 less convex, with 5 setae near distoposterior corner; distoposterior corners of plate 2 and 3 rounded; ventral margin of plate 2 with 1 spine, that of plate 3 with 2 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 8 spines; outer ramus with 6 spines; peduncle with 5 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 7 spines; outer ramus with 5 spines; peduncle with 2 spines. Uropod 3: peduncle not bearing setae; ramus approximately 30 percent length of peduncle, with 2 apical spines.

Telson longer than broad, gently tapered distally; apical margin with small median notch between spine clusters, bearing 9 relatively long spines.

Distribution and ecology. This species is known only from wells of PVC pipe drilled into substrate of Sycamore Creek, 32 km northeast of Phoenix, Arizona. According to Dr. Andrew Boulton (pers. comm.), the material was collected during a study of interstitial

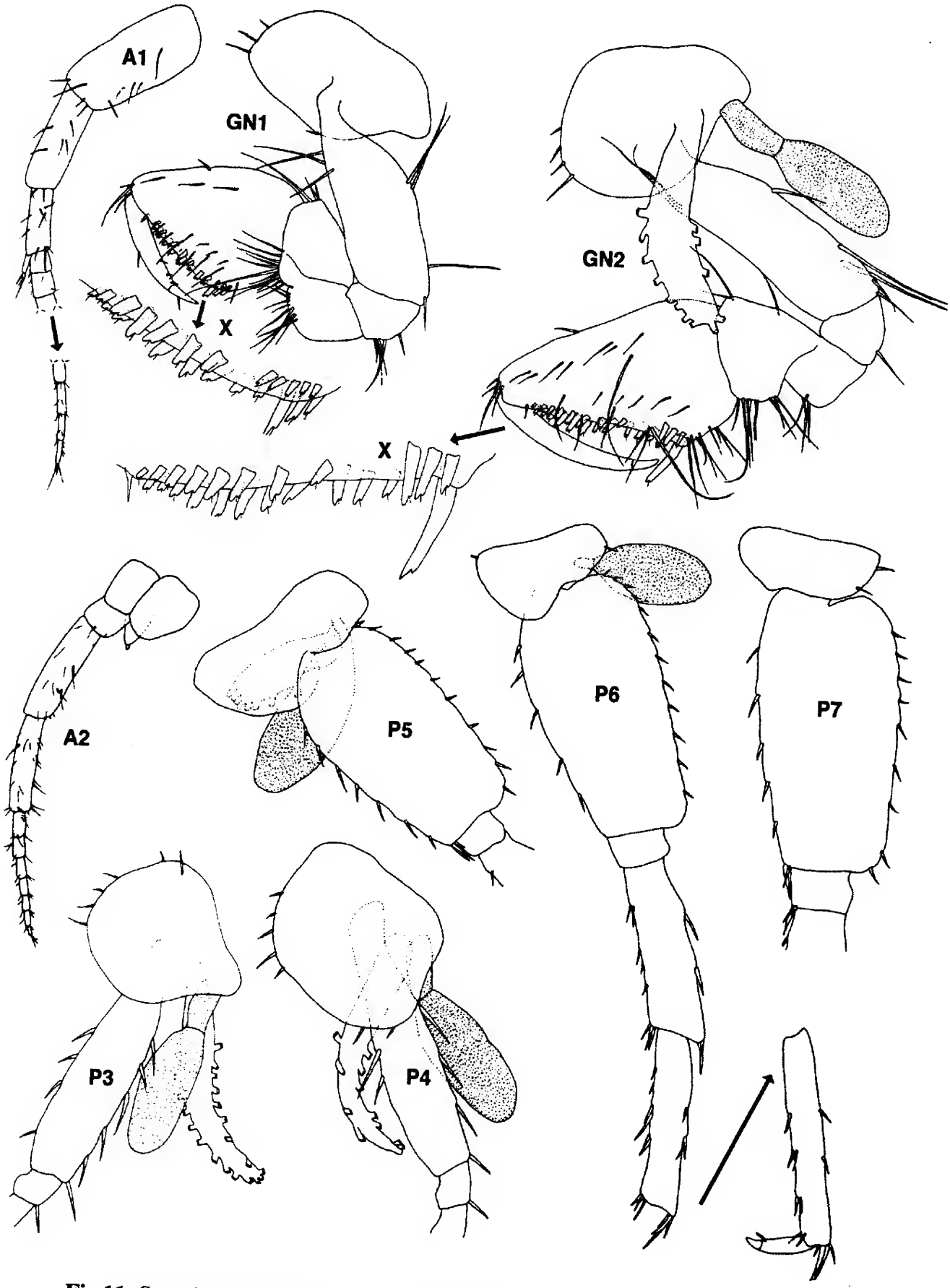

Fig.11. ***Stygobromus trinus*****, n. sp.** Female (7.0 mm). Trinity County, California.

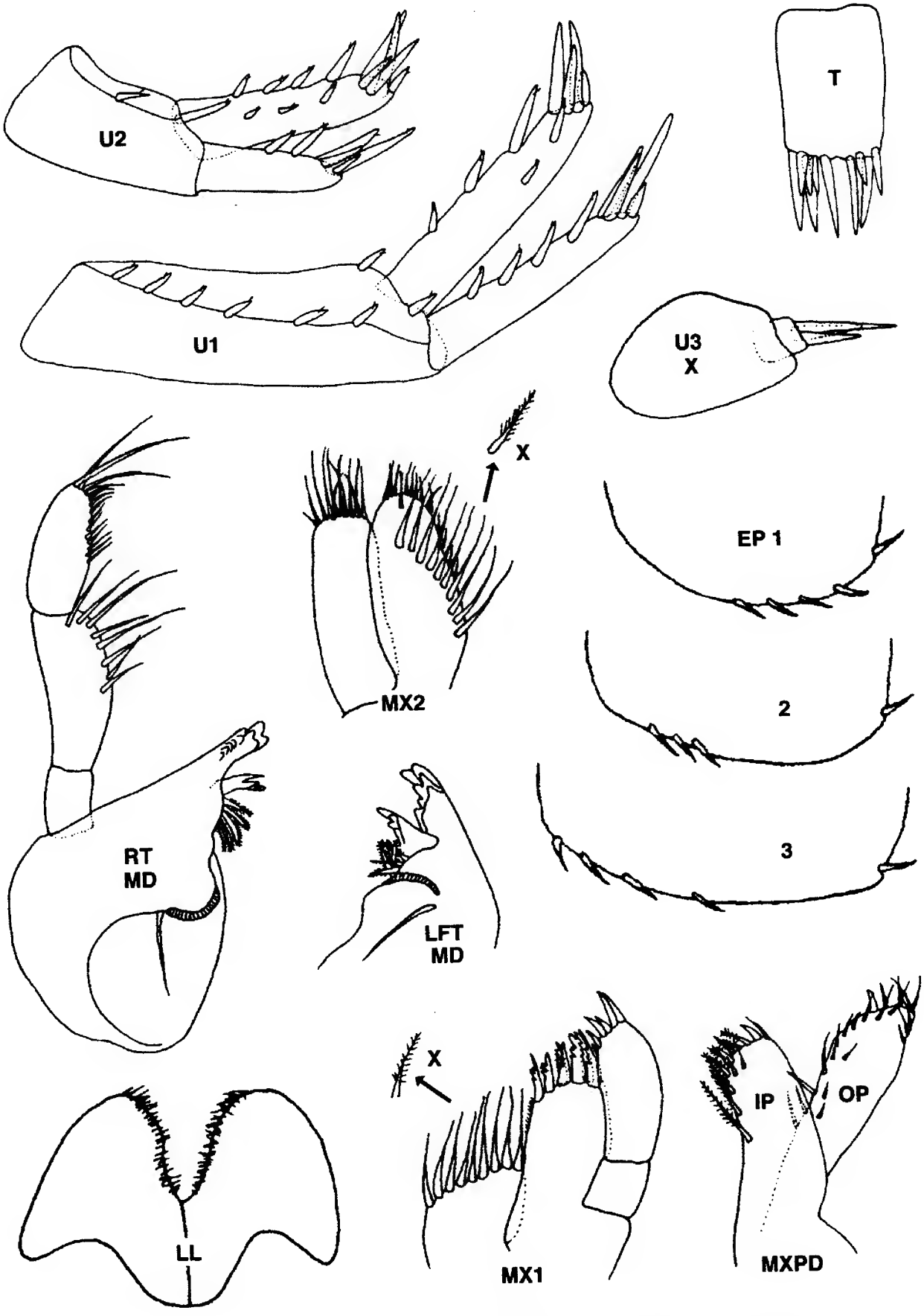

Fig.12. ***Stygobromus trinus*****, n. sp.** Female (7.0 mm). Trinity County, California.

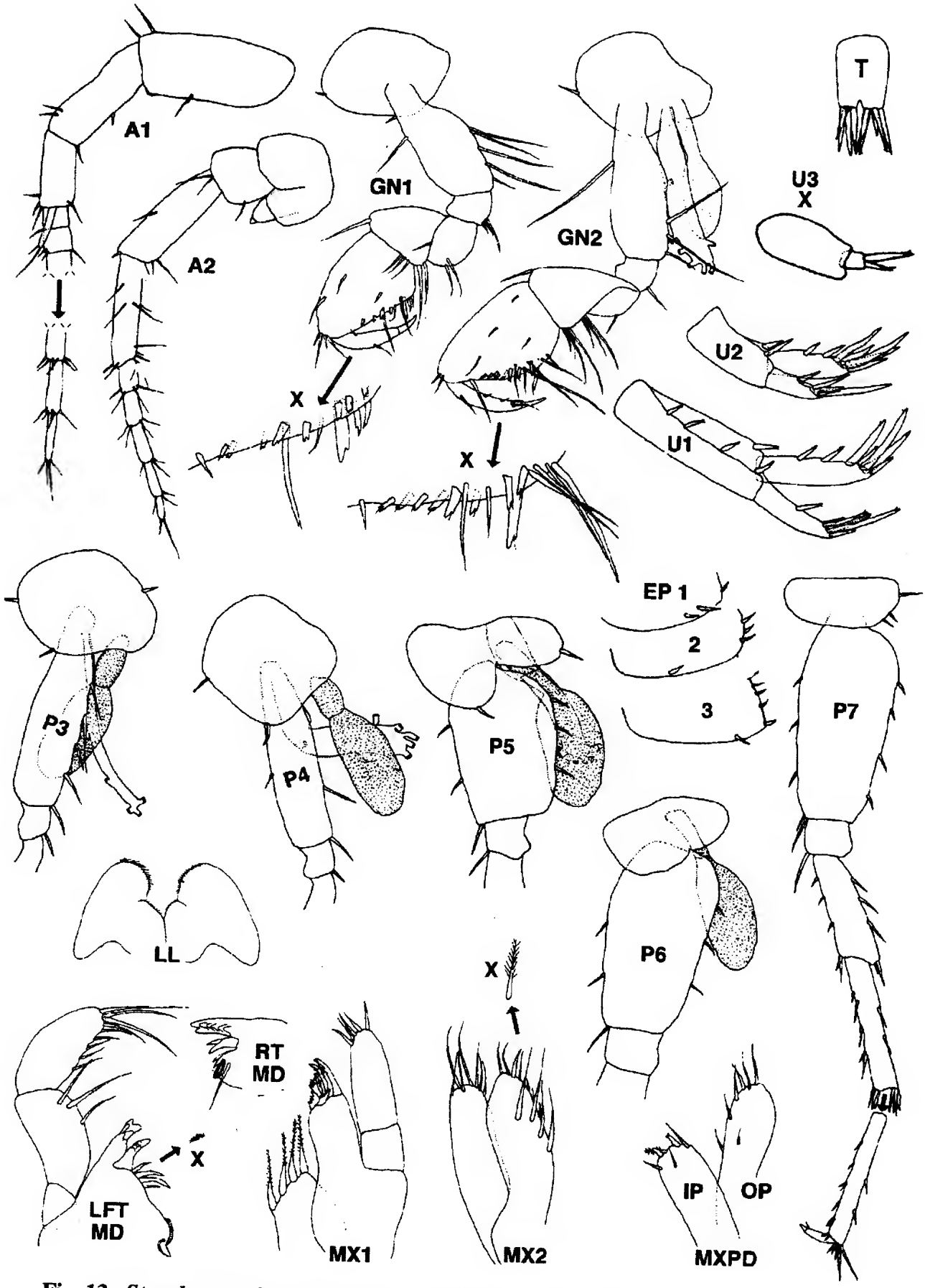

Fig. 13. ***Stygobromus boultoni*, n. sp.** Female (3.7 mm). Maricopa County, Arizona.

fauna utilizing phreatic pumping through PVC wells from a depth of approximately 180 cm.

Etymology. This species is named in honor of its collector, Dr. Andrew Boulton.

Stygobromus duplus, new species
(Figs. 14, 15)

Material examined. WASHINGTON. Spokane Co.: well No. 7 in Spokane Valley, near Millwood, HOLOTYPE ♀ (on slide mounts) (USNM 1000055), L. A. Fusté, 21 Apr. 1981; well No. 5 in Spokane Valley, 1 ♂ paratype, L. A. Fusté, 25 Feb., 1981.

Diagnosis. A medium-sized groundwater species, related to *S. mysticus* and *S. latus* in structure of the gnathopods, but distinguished from those species as follows: gnathopod 2 with shorter posterior margin; bases of pereopods 5-7 much narrower and proportionately longer than other segments; distoposterior lobes of pereopod 5-7 poorly developed or absent; uropods 1 and 2 with more spines on rami and peduncles; telson proportionately broader with long spines. Largest (and only known) ♀ 5.4 mm; largest (and only known) ♂, 5.0 mm.

Female. Antenna 1: 70 percent length of body, 90 percent longer than antenna 2; primary flagellum with 16 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 6 plumose spines; palp segment 2 with row of 7 rather long setae on inner margin; palp segment 3 bearing 2 B setae, 7 D setae, and 3 E setae, lacking A and C setae. Inner lobes of lower lip absent. Maxilla 1: inner plate with 8 apical, plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 10 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 3 plumose spines, and 3 naked setae apically, and 3 coarse setae on inner margin; outer plate with numerous setae along inner margin and 5 setae on or near apex.

Gnathopod 1: propod shorter than propod of gnathopod 2; palm slightly convex and about 35 percent longer than posterior margin, armed with 12 spine teeth in double row; defining angle with 2 spine teeth on outside, but no shorter ones on inside; posterior margin with 2 setae; 6 superior medial setae, in unevern row; few inferior medial setae; dactyl nail rather long and slender; coxa deeper than broad, margin with 2 setae. Gnathopod 2: propod subtriangular, almost 2 times longer than broad; palm armed with 15-16 spine teeth in double row; defining angle with 1 long and 2 shorter teeth on outside, no spine teeth on inside; posterior margin rather short, only about 50 percent length of palm, with 3 sets of mostly doubly inserted setae; 4 superior medial setae; 6 inferior medial setae; coxa about as deep as broad, margin with 4 setae.

Pereopod 3: coxal plate deeper than broad, margin with 5 setae. Pereopod 4: coxal plate deeper than broad, reaching about 35 percent length of basis, margin with 5 setae. Pereopod 6 little longer than pereopod 7, about 70 percent length of body, 25 percent longer than pereopod 5. Pereopods 5-7: bases little broader proximally than distally; posterior margins convex proximally, but not greatly expanded; distoposterior lobes poorly developed or vestigial; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 not greatly elongate, that of pereopod 6 approximately 33 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates somewhat narrowing distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner and 4 spines on ventral margin, that of 2 and 3 also convex, each with 2 setae near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 2 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 75 percent length of peduncle, with 11 spines; outer ramus with 8 spines; peduncle with 11 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 7 spines; outer ramus with 5 spines; peduncle with 5 spines. Uropod 3: ramus short and only approximately 25 percent length of peduncle, with 2 apical spines.

Telson little longer than broad, gently tapered distally; apical margin with tiny median notch between spine clusters, bearing 10-11 mostly longish spines.

Distribution and ecology. To date this species is known only from two specimens from two test wells in the Spokane Valley near Millwood, Spokane County, Washington.

Etymology. The epithet *duplus* is from the Latin, meaning "double or 2 times," which refers to the 2 sets of setae on the posterior margin of the propod of gnathopod 2.

Remarks: The single male specimen was lost in handling after initial examination.

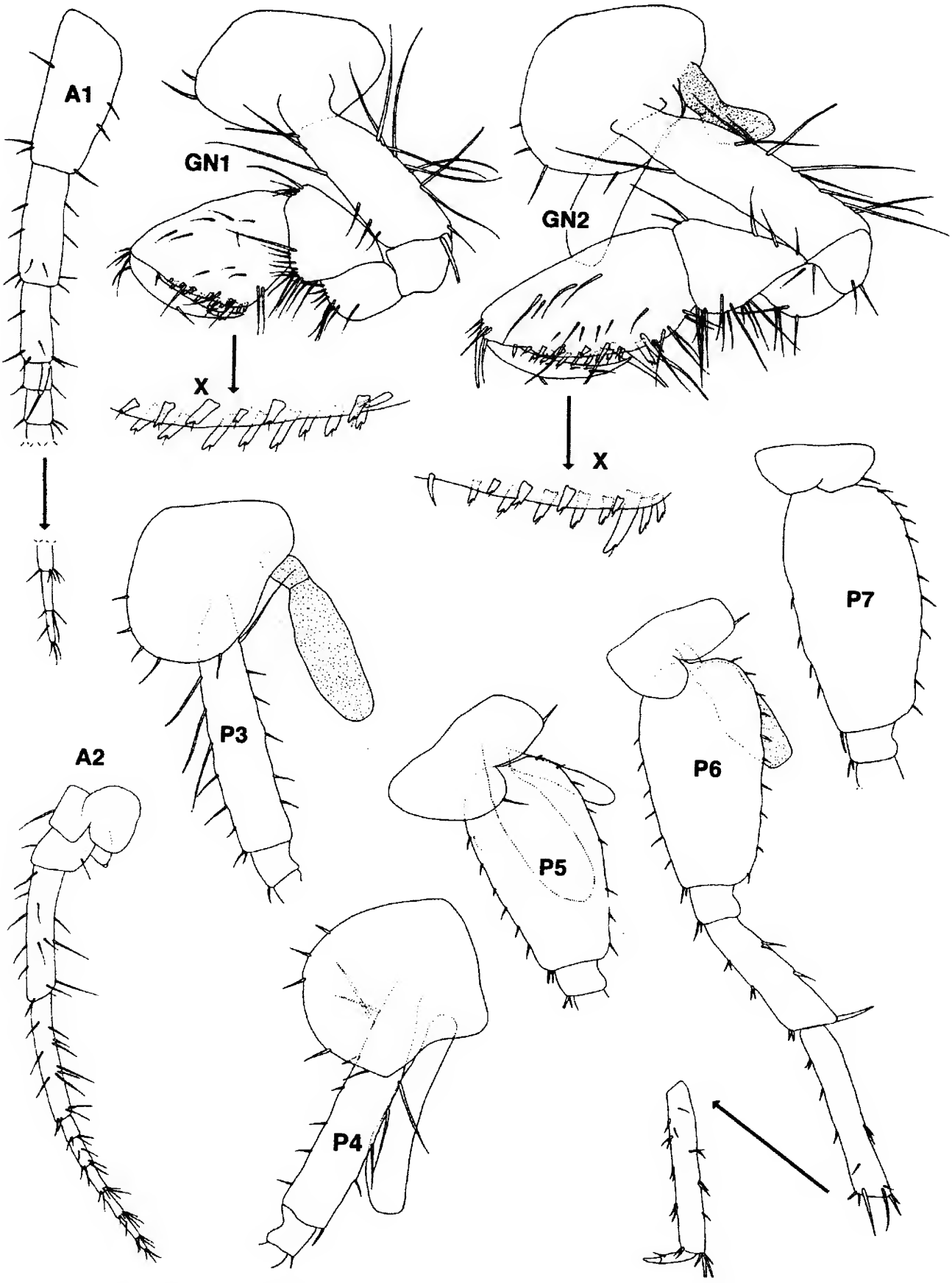

Fig. 14. ***Stygobromus duplus*****, n. sp.** Female (5.4 mm). Spokane County, Washington.

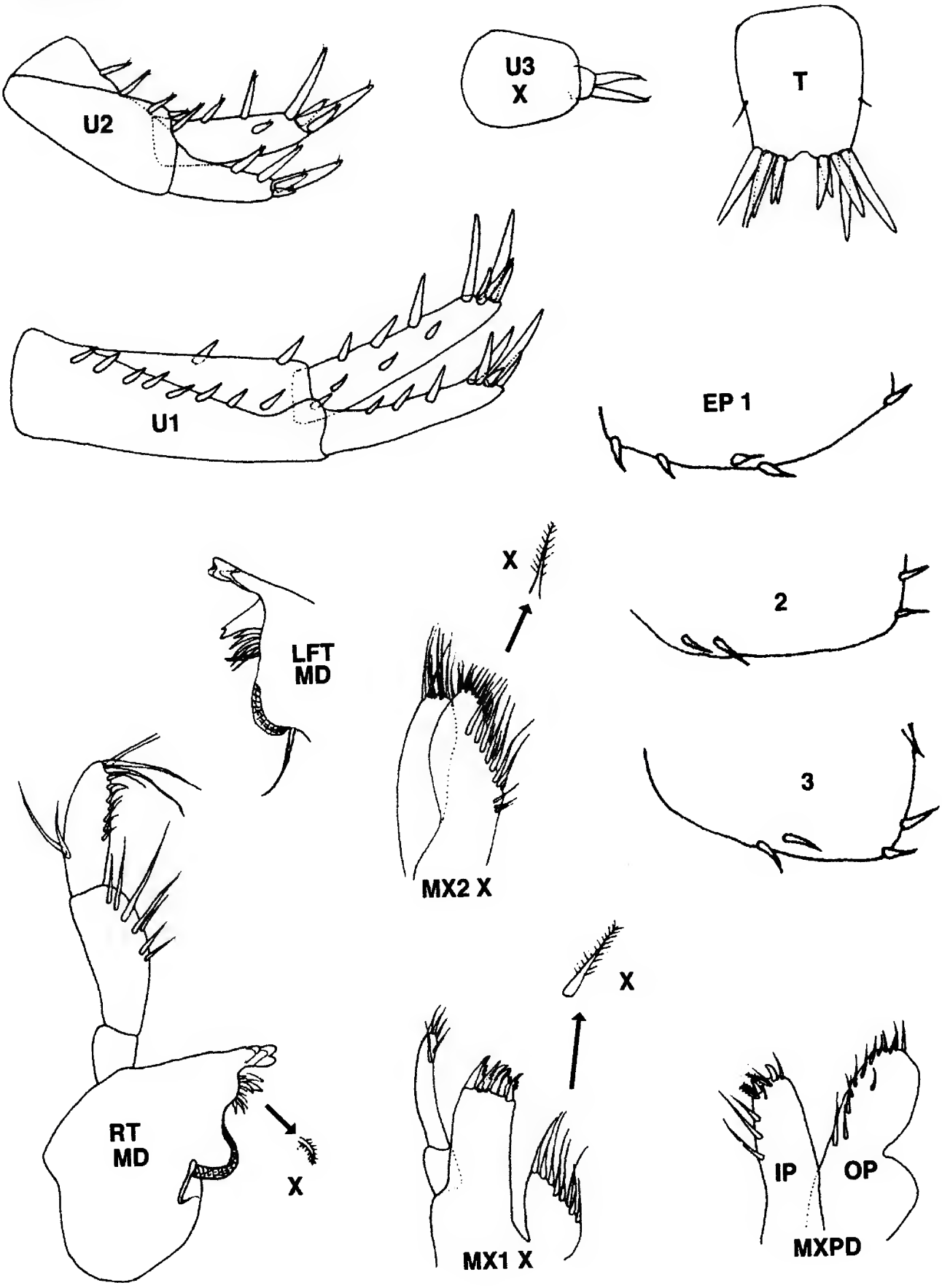

Fig.15. ***Stygobromus duplus*, n. sp.** Female (5.4 mm). Spokane County, Washington.

Stygobromus utahensis, new species
(Fig. 16)

Material examined. UTAH. Duchesne Co.: Pole Creek Cave, about 37 km NNW of Roosevelt, at an elevation of ~2128 m, HOLOTYPE ♀ (USNM 1000074), 70 ♀♀, 13 ♂♂, paratypes, 1 juv., S. J. Peck, 5 Aug. 1979.

Diagnosis. A medium-sized cavernicolous species apparently very similar to *S. arizonensis* in structure of gnathopods and uropod 1-2, but distinguished from this species as follows: coxal plates 3-4 broader than deep; bases of pereopods 6-7 with fewer spines on distoposterior margin; pleonal plates 1-3 lacking spines on ventral margin and fewer setules near distoposterior corner; peduncular process of uropod 1 of male sharply pointed apically; and telson with only slight notch. Largest ♀, 5.5 mm, largest ♂, 4.0 mm.

Female. Antenna 1: 55 percent length of body, 50 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 8-9 plumose spines; palp segment 2 with row of 6 long setae on inner margin; palp segment 3 bearing 1 B seta, 9 D setae, and 3 setae E, lacking both A and C setae. Inner lobes of lower lip vestigial. Maxilla 1: inner plate with 8 apical, plumose setae; palp with 4 stiff setae subapically. Maxilla 2: inner plate with oblique row of 7 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 1 plumose spine, 1 naked seta apically, and 3 setae on inner margin; outer plate with setae on inner margin and 4-5 on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight or slightly concave, 2 times longer than posterior margin, armed with 17 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; 4 doubly inserted superior medial setae; 3 singly inserted inferior medial setae; dactyl nail rather long and sharply pointed; coxa about 2 times broader than deep, margin with 2 setae. Gnathopod 2: propod longer than broad; palm straight or slightly convex, strongly oblique, armed with 13 spine teeth in double row; defining angle with 1 spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 30 percent length of palm, with 2 sets of doubly inserted setae; 7 superior medial setae, most doubly inserted; 5 inferior medial setae, most singly inserted; coxa about as broad as deep, margin with 3 setae.

Pereopod 3: coxal plate slightly broader than deep, margin with 3 setae. Pereopod 4: coxal plate broader than deep, reaching about 30 percent length of basis, margin with 2 setae. Pereopod 6 little longer than pereopod 7, about 58 percent length of body, 20 percent longer than pereopod 5. Pereopods 5-7: bases little broader proximally than the distally; posterior margins convex; distoposterior lobes poorly developed and almost indistinct; anterior and posterior margins with 2-4 spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 about 35 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates little expanded distally.

Pleonal plates: posterior margins of plate 1 - 3 convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plates 1, 2 and 3 lacking spines. Uronites free. Uropod 1: inner ramus subequal to outer ramus, about 60 percent length of peduncle, with 8 spines; outer ramus with 8 spines; peduncle with 6 spines. Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 8 spines; outer ramus with 5 spines; peduncle with 3 spines. Uropod 3: peduncle not bearing small setae; ramus approximately 30 percent length of peduncle, with 2 apical spines.

Telson little longer than broad, gently tapered distally; apical margin with small median notch between spine clusters, bearing 8 relatively long spines.

Male. Differing from female as follows: Gnathopod propods smaller and shorter, palm of propod 2 longer in relation to posterior margin and with fewer teeth on palmar margin. Uropod 1: peduncular process 10 percent length of outer ramus, sharply pointed distally, upper margin minutely serrate; inner ramus with 5 spines; peduncle with 6 spines. Uropod 2: inner ramus with 5 spines, peduncle with 2 spines. Telson with 8 apical spines.

Distribution and ecology. This species is known only from its type-locality.

Etymology. The species is named for the state of Utah.

Stygobromus interstitialis, new species
(Figs. 17, 18)

Material examined. COLORADO. El Paso Co.: hyporheicin deep gravel alluvium of Monument Creek below Palmer Lake, HOLOTYPE ♀ (USNM 1000063), 2 ♂♂ and 2 ♀♀ paratypes, J. V. Ward, 5 Oct 1980; Monument Creek, ca. 30 km N of Colorado Springs, 1 ♂, J. V. Ward, 27 July 1979;

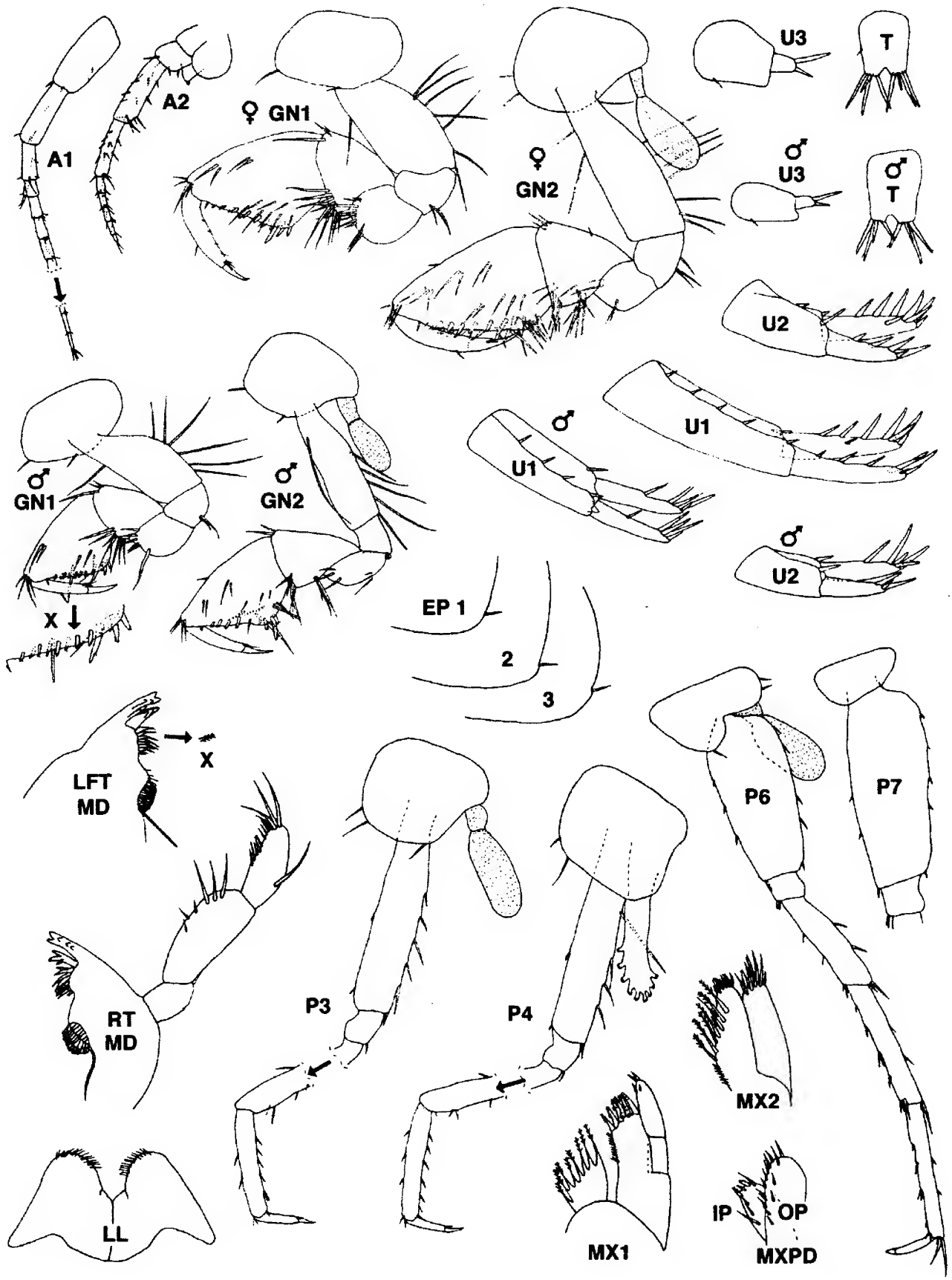

Fig.16. *Stygobromus utahensis*, n. sp. Female (5.5 mm); male (4.0 mm). Duchesne County, Utah.

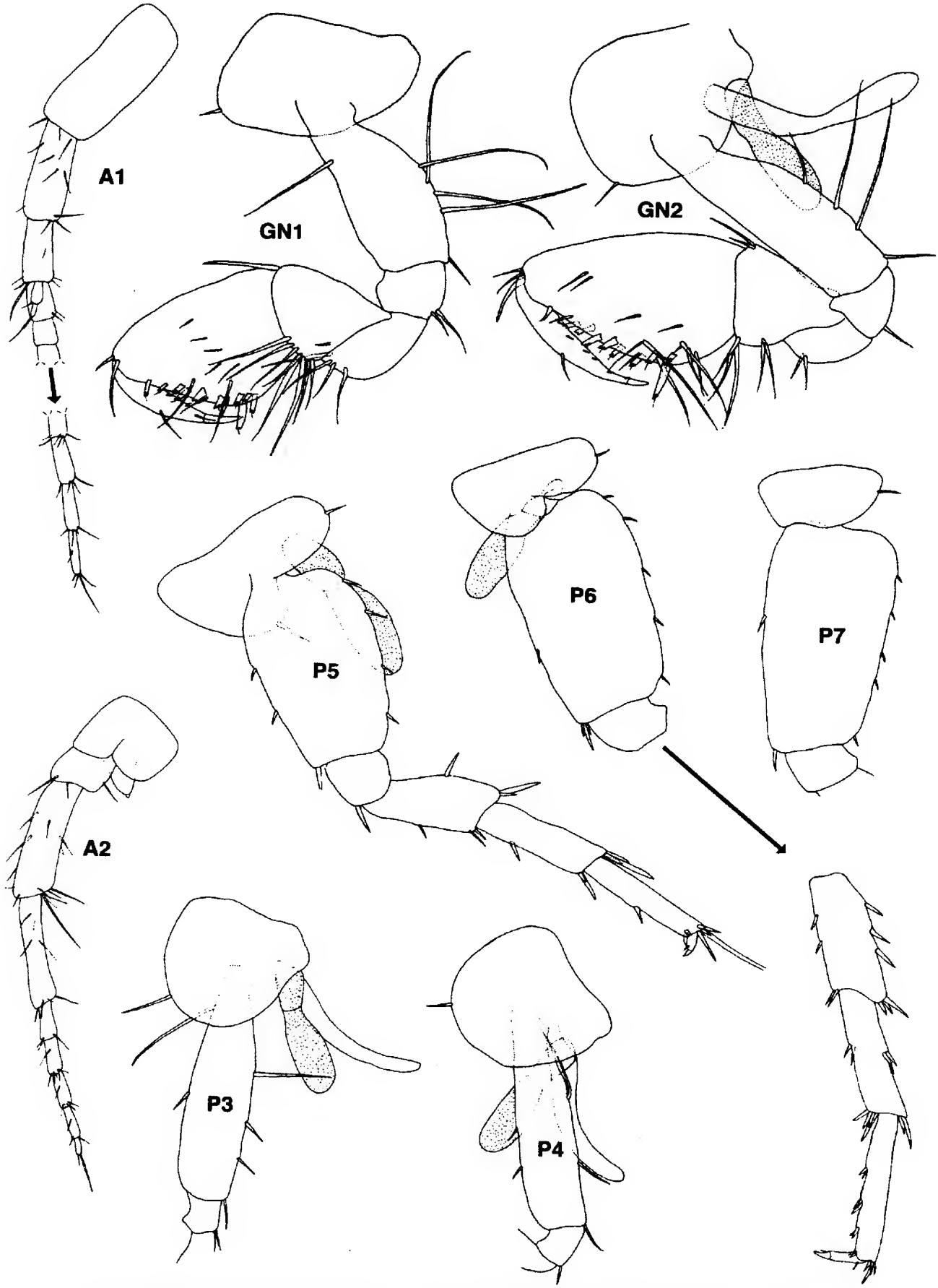

Fig. 17. ***Stygobromus interstitialis*****, n. sp.** Female (3.6 mm). El Paso County, Colorado.

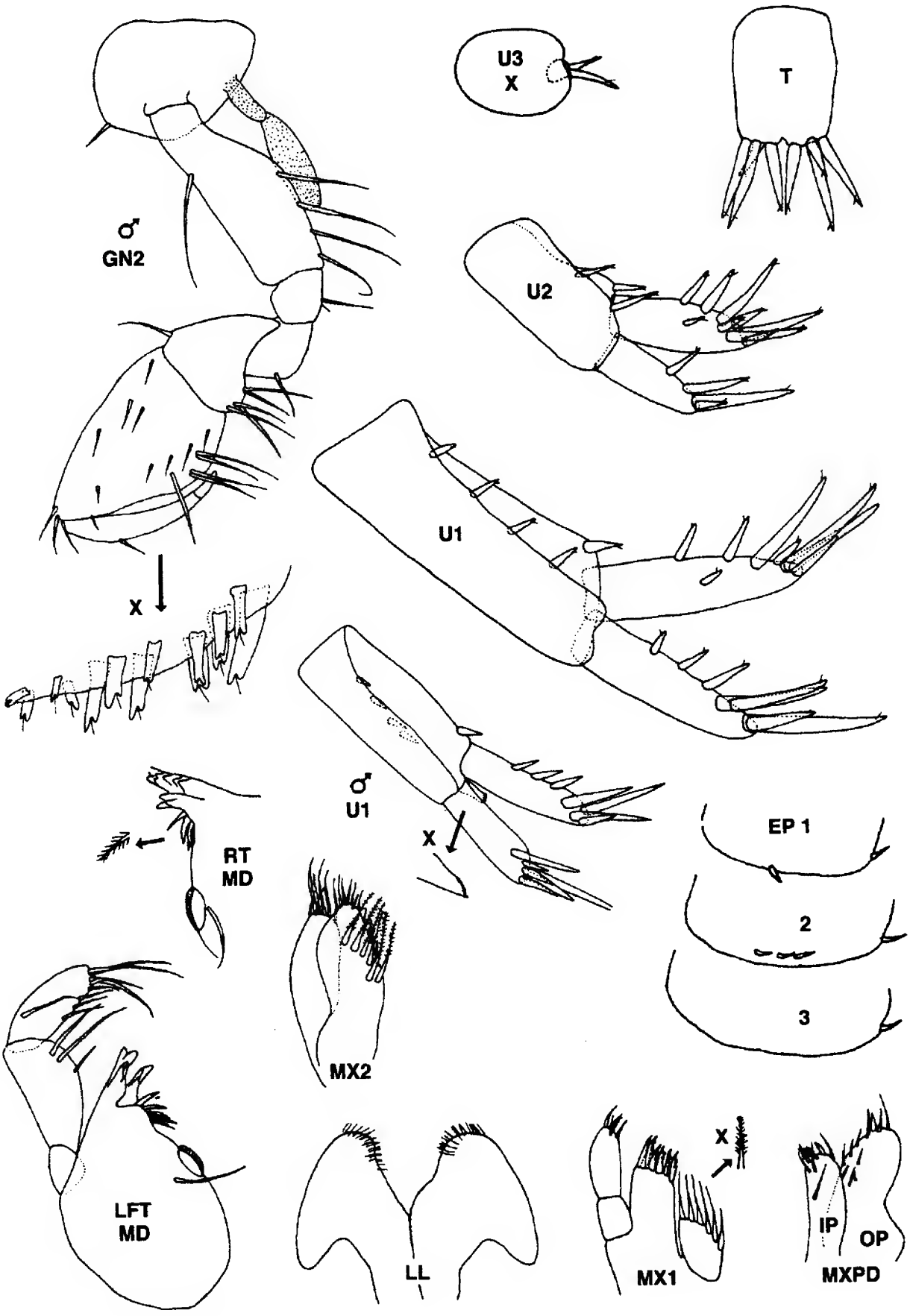

Fig.18. ***Stygobromus interstitialis*****, n. sp.** Female (3.6 mm); male (3.0 mm) El Paso Co., Colorado.

Monument Creek in Colorado Springs, 1 ♀, S. P. Canton, 4 Nov. 1987.

Diagnosis. A small groundwater species, very similar to *S. coloradensis* but distinguished as follows: maxillae 1 and 2 with more setae on inner plates; posterior margin of palm of propod 2 shorter; pleonal plate 3 lacking ventral spines; uropods 1-2 with more long, thick spines on rami; uropod 3 with very short ramus; telson with longer apical spines and slight notch between spine clusters. Largest ♀, 3.6 mm; largest ♂, 3.0 mm.

Female. Antenna 1: 50 percent length of body, 55 percent longer than antenna 2; primary flagellum with 12 segments. Antenna 2: flagellum with 5 segments.

Mandibles: spine row with 4-5 plumose spines; palp segment 2 with row of 3 setae on inner margin; palp segment 3 bearing 1 B seta, 4 C setae, and 4 E setae, lacking both A and D setae. Inner lobes of lower lip vestigial/absent. Maxilla 1: inner plate with 6 apical, plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 2 plumose spines, 1 naked seta apically, and 3 plumose spines on inner margin; outer plate with short setae on inner margin, 3 lightly plumose setae and 1 small bladelike spine on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight or slightly concave medially, approximately 2 times longer than posterior margin, armed with 10 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin without setae; 4-5 singly inserted medial setae, dactyl nail rather long; coxa about 25 percent broader than deep, margin with 1 seta. Gnathopod 2: propod longer than broad; palm straight and armed with 9 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 1 set of triply inserted setae; 2 superior medial setae, 2 singly inserted inferior medial setae; dactyl nail relatively short; coxa little broader than deep, margin with 1 seta.

Pereopod 3: coxal plate about as broad as deep, margin with 1 seta. Pereopod 4: coxal plate about as broad as deep, reaching about 25 percent length of basis, margin with 1 seta. Pereopod 6 little longer than pereopod 7, about 50 percent length of body, 36 percent longer than pereopod 5. Pereopods 5-7: bases about as broad proximally as distally; posterior margins convex; distoposterior lobes poorly developed; anterior and posterior margins with variable but few spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 approximately 30 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from pereopod 7. Brood plates slightly narrowing distally, but not setose (fully mature) in material examined.

Pleonal plates: posterior margins of plate 1 - 2 weakly convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 1 with 1 spine, that of plate 2 with 3 spines. Uronites free. Uropod 1: inner ramus slightly longer than outer ramus, about 75 percent length of peduncle, with 8 spines; outer ramus with 7 spines; peduncle with 5 spines. Uro-pod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 9 spines; outer ramus with 4 spines; peduncle with 3 spines. Uropod 3: peduncle not bearing setae; ramus tiny, approximately 20 percent length of peduncle, with 2 apical spines.

Telson longer than broad, apical margin with tiny median notch between spine clusters, bearing approximately 8 relatively long spines.

Male. Differing from female as follows: gnathopod propods smaller and narrower, palm of propod 2 longer in comparison to posterior margin, with more teeth on palmar margin. Uropod 1: peduncular process 30 percent length of outer ramus, sharply pointed distally, inner ramus with 7 spines; outer ramus with 5 distal spines; peduncle with 5-6 spines. Uropod 2: inner ramus with 9-10 spines, peduncle with 3-4 spines. Telson with 9 apical spines.

Distribution and ecology. This species is recorded from hyporheic habitats in the deep gravel alluvium of Mounument Creek at three different sites (see "material examined") in El Paso Co., Colorado.

Etymology. The epithet *interstitialis* is from the Latin, meaning "interstitial," in reference to the habitat of this species.

Stygobromus puteanus Holsinger, 1974

Stygobromus puteanus Holsinger, 1974: 11-13, figs. 4-5 [type-locality: an unnamed well near Three Forks, Gallatin Co., Montana].

Diagnosis. A medium-sized subterranean species simi-

lar to *S. tritus* but distinguished from that species by the straight to slightly convex palms of gnathopodal propods, broader bases of pereopods 5-7; and having more apical spines on uropod 3 and telson. Largest ♀, 6.5 mm; ♂ unknown (see Holsinger 1974).

Distribution and ecology. This species is known only from its type locality.

Stygobromus pennaki Ward, 1977

Stygobromus pennaki Ward, 1977: 458-461, figs. 3-5 [type-locality: hyporheic in North Fork of the South Platte River, Jefferson Co., Colorado].

Material examined. COLORADO. Arapahoe Co.: interstitial waters of "shore zone" with Bou-Rouch pump in South Platte River, Littleton (ca. 2.5 km below Chatfield reservoir), 1♀, 1♂, S. P. Canton, 9 Feb. 1988; Jefferson Co.: hyporheic habitats in North Fork of South Platte River by S. P. Canton as follows: 0.48 km W of S. Platte, 2♀♀, 26 Mar. 1985; 2♀♀, 5 Apr. 1985 and 5♀♀, 9 Apr. 1985; 0.8 km W. S. Platte, 3♀♀, 1♂, 5 Apr. 1985; behind S. Platte Hotel, 5♀♀, 5 Apr. 1985, 7 ♀♀, 9 Apr. 1985, and 14 ♀♀, 5 Nov. 1985; 100 m downstream from jct. with N. Fork, 3 ♀♀, 5 Apr. 1985; near gaging station in S. Platte, 2 ♀♀, 9 Apr. 1985.

Diagnosis. A small hyporheic species, apparently related to *S. puteanus* but distinguished by longer gnathopod propod 1 with more oblique palm; more teeth on palmar margin; fewer marginal setae on coxal plates 3 and 4; more spines on posterior margin of pleonal plates, fewer spines on ventral margins; and uropod 3 with proportionately larger ramus. Largest ♀, 4.3 mm; largest ♂, 4.1 mm.

Distribution and ecology. This species is known from hyporheic habitats in the North Fork of South Platte River, Jefferson County, and interstitial waters of the shore zone, Arapahoe County, Colorado (see also Pennak and Ward 1986). As noted later, this species was often collected with *S. coloradensis* in hyporheic habitats in the South Platte River.

Stygobromus urospinatus, new species
(Figs. 19, 20)

Stygobromus sp. A.—Ward & Holsinger, 1981: 64-67.

Material examined. COLORADO. Larimer Co.: Bellvue Spring, about 1.6 km SE of Bellevue, HOLOTYPE ♀ (USNM 1000073), 13 ♀♀ paratypes, J. V. Ward, 15 Sept. 1977; 1 ♂, 16 ♀♀, J. V. Ward, 2 Apr. 1978; 3 ♂♂, 3 ♀♀, J. V. Ward, 29 Jan. 1978; Redstone spring no. 1, west of Horsetooth Reservoir, 1 ♂, J. V. Ward, 30 Oct 1976; spring at base of Spring Canyon Dam of Horsetooth Reservoir, 9 ♀♀, J. V. Ward, 28 Apr. 1975.

Diagnosis. A medium-sized groundwater species similar to *S. holsingeri* but differing as follows: palms of gnathopods 1 and 2 straight; coxal plates of pereopods 3 and 4 deeper than broad; pleonal plates 1-3 with fewer ventral spines but more setules on posterior margin; uropods 1-3 more heavily spinose; and telson with numerous and longer spines on apical margin. Largest ♀, 7.0 mm; largest ♂, 6.0 mm.

Female. Antenna 1: 46 percent length of body, 8 percent longer than antenna 2; primary flagellum with 12 segments. Antenna 2: flagellum with 8 segments.

Mandibles subequal: spine row with 8 plumose spines; palp segment 2 with about 12 long setae on inner margin, segment 3 bearing 1 long B seta, 2 C setae, approximately 14 D setae, and 5 E setae, lacking A setae. Inner lobes of lower lip vestigial or absent. Maxilla 1: inner plate with 10 apical, plumose setae; palp with 13 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 11 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 3 plumose spines, 1 naked seta apically and 2 plumose setae on inner margin; outer plate with setae on inner margin and 5 setae on or near apex.

Gnathopod 1: propod subequal in size to gnathopod 2; palm straight and nearly 2 times longer than posterior margin, armed with 26 spine teeth in double row; defining angle with 3 spine teeth on outside, 4 shorter ones on inside; posterior margin without setae; bearing single superior medial seta and lacking inferior medial setae; dactyl nail short; coxa approximately 2 times broader than deep, margin with 3 setae. Gnathopod 2: propod longer than broad; palm long and straight, armed with 29 spine teeth in double row; defining angle with 1 long spine tooth on outside, 3 shorter spine teeth on inside; posterior margin relatively short, only approximately 33 percent length of palm, with 3 sets of setae, 2 mostly triply inserted; bearing 4 doubly inserted superior setae and 4 singly inserted inferior medial setae; coxa little broader than deep, margin with 5 setae.

Pereopod 3: coxal plate broader than deep, margin with 4 setae. Pereopod 4: coxal plate broader than deep, reaching approximately 25 percent length of basis, margin with 6 setae. Pereopod 6 little longer than pereopod 7, about 70 percent length of body, 33 percent longer than pereopod 5. Pereopods 5-7: bases narrow,

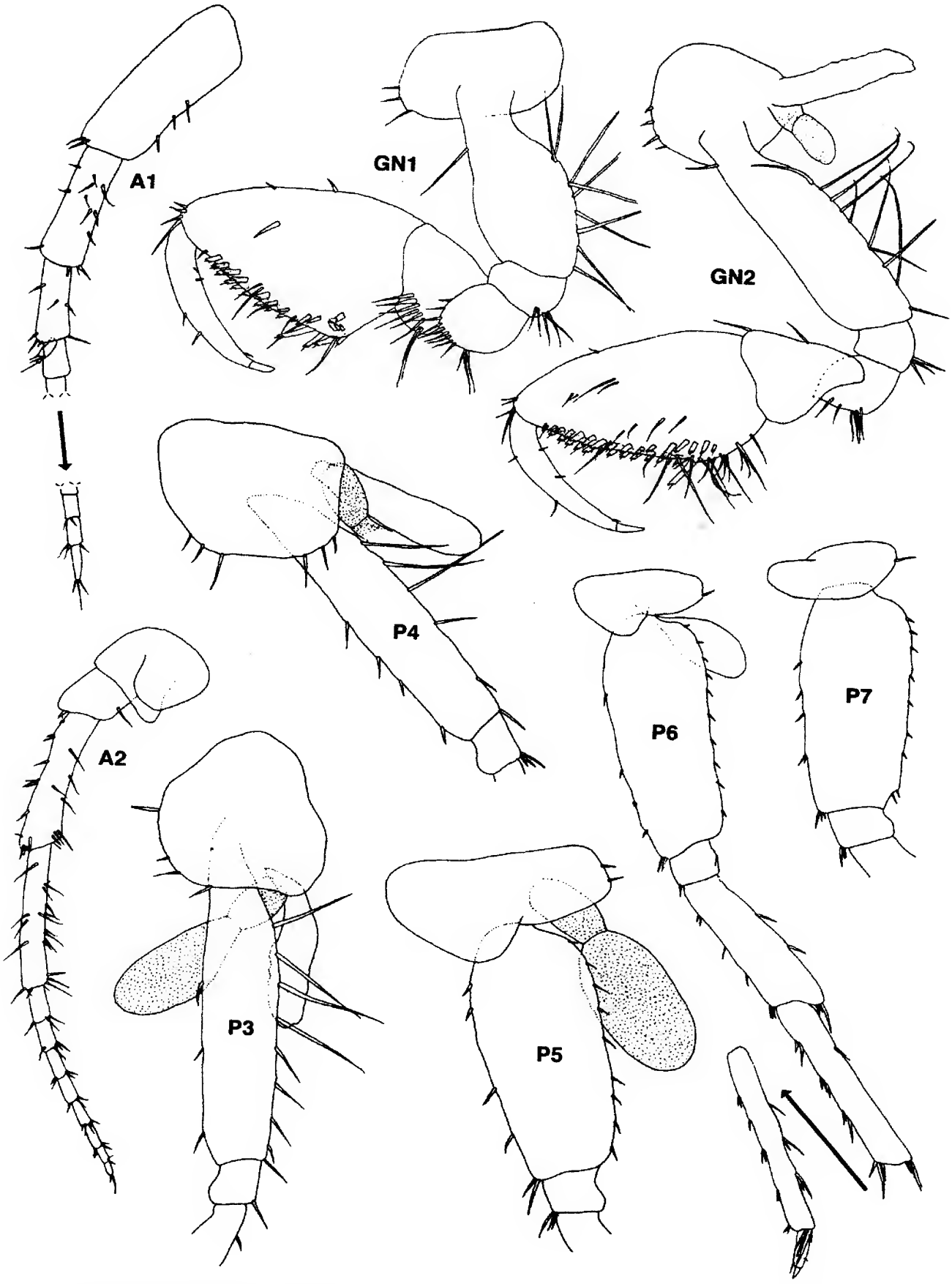

Fig. 19. ***Stygobromus urospinatus*, n. sp.** Female (7.0 mm). Larimer County, Colorado.

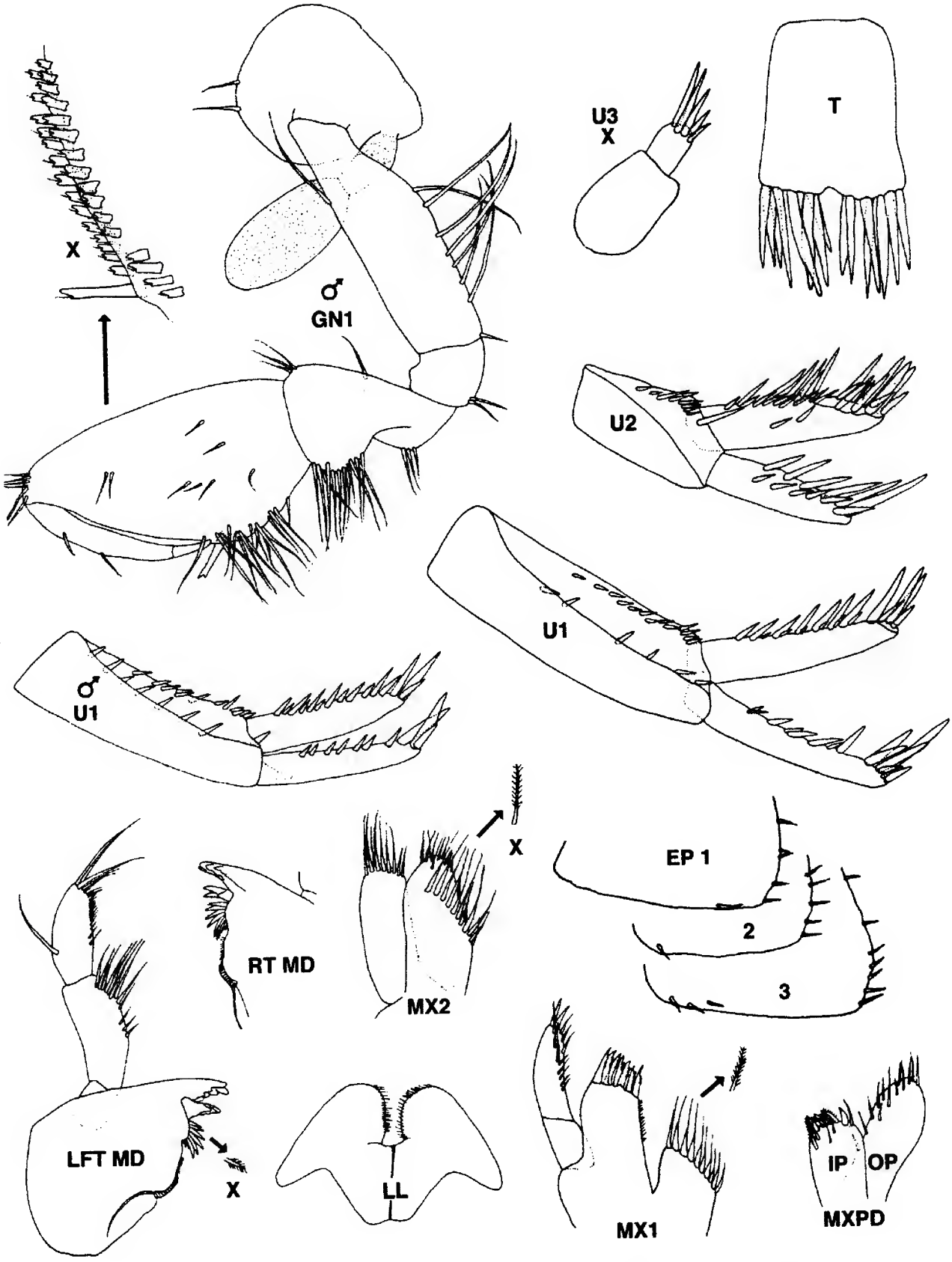

Fig. 20. *Stygobromus urospinatus*, n. sp. Female (7.0 mm); male (6.0 mm) Larimer County, Colorado.

about as broad proximally as distally; posterior margins nearly straight; distoposterior lobes almost indistinct, not broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 typically about 25 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from pereopod 7.

Pleonal plates: posterior margins weakly convex, with 7 setules on posterior margin of plate 3 and 5 setules on margins of plates 1 and 2; distoposterior corner indistinct; ventral margin of plates 1 and 2 bearing 1 spine, that of plate 3 bearing 3 spines. Urontes free. Uropod 1: heavily spinose, especially inner ramus; inner ramus subequal in length to outer ramus, about 70 percent length of peduncle, with 18 long spines; outer ramus with 15 spines; peduncle with 19 long, strout spines. Uropod 2: heavily spinose overall, inner ramus longer than outer ramus and peduncle, with 30 long, strout spines; outer ramus with 14 mostly long spines; peduncle with 10 spines. Uropod 3: peduncle without setae; ramus approximately 50 percent length of peduncle, with 5 apical spines (3 relatively long).

Telson longer than broad, little broader distally, apical margin with tiny median notch between spine clusters, bearing 16 relatively long, strout spines.

Male. Differing from female as follows: gnathopod propods slightly broader; palm of propod 2 slightly longer in comparison with posterior margin and bearing more sets of setae. Uropod 1: peduncular process 25 percent length of outer ramus, tapered to a point distally, inner ramus with 15-17 long spines; peduncle with 20 spines. Uropod 2: inner ramus with 28-35 long spines, peduncle with 10-12 spines. Telson with 16-19 apical spines.

Distribution and ecology. This species is recorded from Bellvue Spring, the type-locality, and two other springs near Horsetooth Reservoir, west of Ft. Collins. It was collected together with 1 specimen of *S. holsingeri* on 30 Oct. 1976 from Redstone Spring no. 1. All sites are in Larimer County.

Etymology. The epithet *urospinatus* is from the Latin, meaning "spines on uropods," in reference to the heavily spinose uropods of this species.

Stygobromus coloradensis Ward, 1977

Stygobromus coloradensis Ward, 1977: 452-456, figs. 1-2 [type-locality: hyporheic in North Fork of the South Platte River, Jefferson Co., Colorado].

Materialexamined. COLORADO. Jefferson Co.: hyporheic in North Fork of South Platte River, by S. P. Canton as follows: upstream of confluence with mainstream, 1 ♀, 4 Apr. 1984; 0.48 km W of S. Platte, 17 ♀♀, 26 Mar. 1985 and 3 ♀♀, 5 Apr. 1985; 0.8 km W of S. Platte, 17 ♀♀, 5 Apr. 1985; just below jct. with N. Fork, S. Platte, 1 ♀, 5 Apr. 1985; 100 m downstream from jct. with N. Fork, 2 ♀♀, 5 Apr. 1985; upstream from Dam Rock, 7 ♀♀, 9 Apr. 1985; behind S. Platte Hotel, 17 ♀♀, 1 ♂, 9 apr. 1985; just upstream from jct. with N. fork, 2 ♀♀, 9 Apr. 1985; near gaging station in S. Platte, 25 femlae, 9 Apr. 1985; S. Platte, 2 ♀♀, 9 Apr. 1985.

Diagnosis. A very small hyporheic species, distinguished by possession of 4 apical plumose setae on inner plate of maxilla 1; oblique row of 4 plumose setae on margin of inner plate of maxilla 2; gnathopodal propods small and robust, palmar margins slightly oblique and distinctly serrated, few teeth on palmar margin; uropod 3 with 1 short and 1 longer spine. Largest ♀, 3.3 mm; largest ♂, 3.0 mm.

Distribution and ecology. This species is known from hyporheic habitats in the North Fork of South Platte River, Jefferson Co., Colorado (see Pennak and Ward 1986). In most collections made in March, April and November 1985, this species was found together with *S. pennaki.*

Stygobromus blinni, new species
(Fig. 21)

Material examined. ARIZONA. Coconino Co.: Roaring Springs Cave, on the north rim of the Grand Canyon near Bright Angel Trail and Bright Angel Creek, HOLOTYPE ♀ (USNM 1000050), 2 ♀♀ paratypes, D. Blinn, 28 Sept. 1994.

Diagnosis. A medium-sized cavernicolous species, very similar to *S. arizonensis* in gnathopods and *S. holsingeri* in uropod 2, but distinguished from these 2 species by the following: maxilla 2 with fewer setae on inner plate; maxilliped with bladelike spines on outer plate (unlike *S. holsingeri*); coxal plate 4 broader than deep; bases of pereopods 5-7 narrow and with more setae on the margin; uropod 1 with more long and stout spines on rami and peduncle; uropod 2 with more long and stout spines on rami; uropod 3 ramus smaller; telson notched slightly. Largest ♀, 6.0 mm, ♂ unknown.

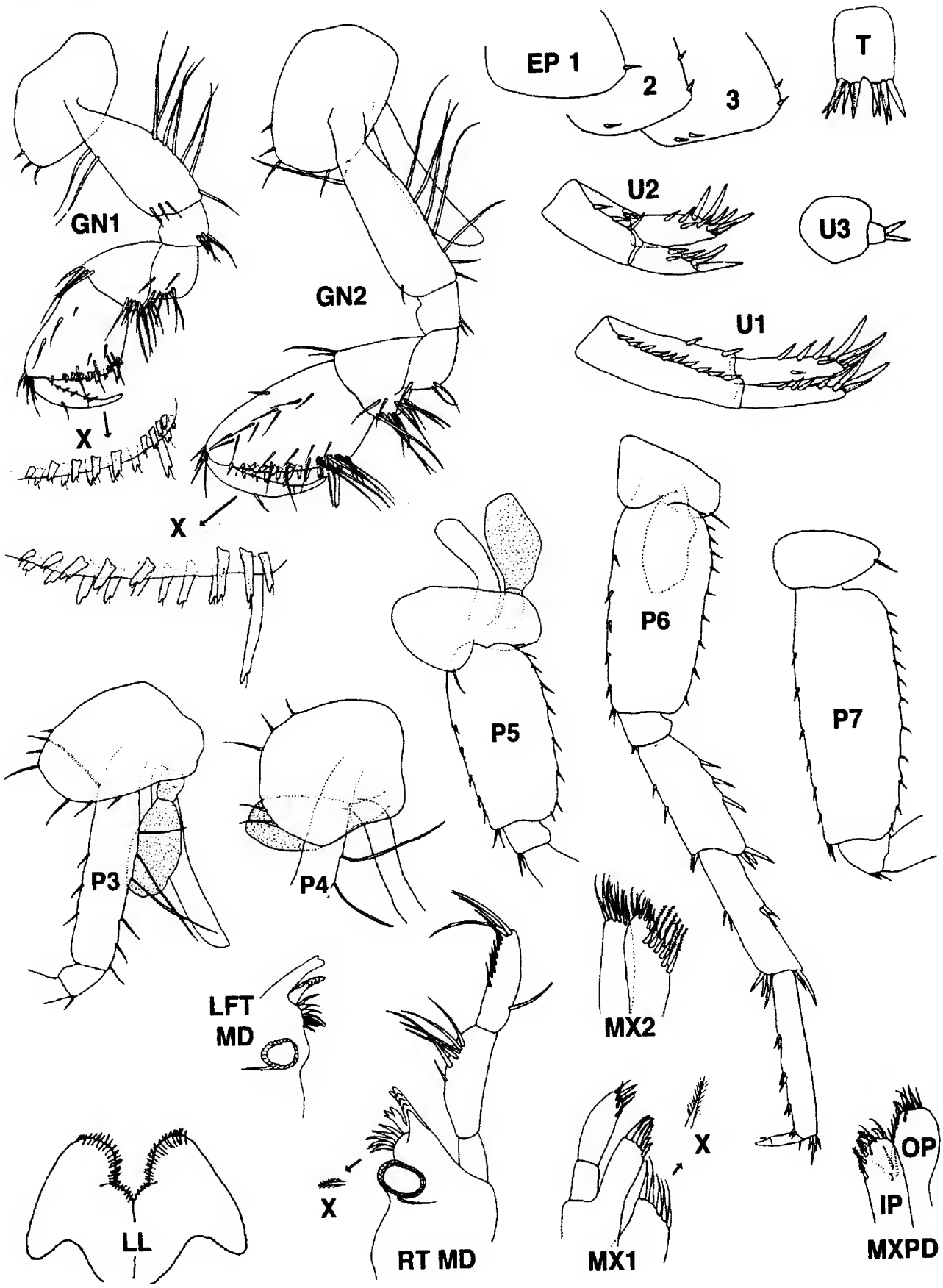

Fig. 21. ***Stygobromus blinni*, n. sp.** Female (5.8 mm). Coconino County, Arizona.

Female. Antenna 1: 67 percent length of body, 25 percent longer than antenna 2; primary flagellum with 16 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 7-8 plumose spines; palp segment 2 with row of 6 rather long setae on inner margin; palp segment 3 bearing 1 long B seta, 5 C setae, few D setae, 4 E setae, lacking A setae. Inner lobes of lower lip vestigial or absent.Maxilla 1: inner plate with 5 apical, plumose setae; palp with 7 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 3 plumose spines, and 2 naked setae apically, and 2 plumose spines on inner margin; outer plate with setae on inner margin and apex, and 1 lightly plumose spine on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight and little longer than posterior margin, armed with 17 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; superior medial setae 3; 2 inferior medial setae; dactyl nail rather long; coxa rather narrow, deeper than broad, margin with 3 setae. Gnathopod 2: propod oblique, deeper than broad; palm straight and armed with 17 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 1 set of setae near defining angle; 8 - 9 superior medial setae, doubly inserted; 4 singly-inserted inferior medial setae; coxa deeper than broad, margin with 4 setae.

Pereopod 3: coxal plate deeper than broad, margin with 6 setae. Pereopod 4: coxal plate relatively broad and deep, reaching about 33 percent length of basis, margin with 5 setae. Pereopod 6 little longer than pereopod 7, about 80 percent length of body, 15 percent longer than pereopod 5. Pereopods 5-7: bases as broad proximally as distally; posterior margins slightly convex; distoposterior lobes weakly developed, that of 7 indistinct; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 about 45 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates somewhat narrowing distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner, that of 2 and 3 less convex, each with 2 setae near distoposterior corner; distoposterior corners rounded; ventral margin of plate 2 with 1 spine, that of plate 3 with 2 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 75 percent length of peduncle, with 8-9 spines; outer ramus with 8-9 spines; peduncle with 12 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 10 spines; outer ramus with 6 spines; peduncle with 4 spines. Uropod 3: peduncle usually lacking small setae; ramus approximately 30 percent length of peduncle, with 2 apical spines.

Telson little longer than broad, apical margin with small median notch between spine clusters, bearing 10-11 relatively long spines.

Distribution and ecology. This species is only known from its type-locality. It was collected from a slow-moving stream with a fine sediment/gravel substrate, about 1.6 km inside the cave (Dean Blinn, pers. comm.).

Etymology. It is pleasure to name this species for its collector, Dr. Dean Blinn.

Stygobromus holsingeri Ward, 1977

Stygobromus holsingeri Ward, 1977: 461-465, figs. 6-8 [type-locality: small unnamed spring/seep, 3.2 km W. of Ft. Collins, Larimer Co., Colorado]. Ward and Holsinger 1981: 64-65.

Material examined. COLORADO. Larimer Co.: several habitat types associated with interrupted stream drainage near Horsetooth Reservoir, W of Ft. Collins, approximately 240 specimens, J. V. Ward, May 1976 - Jan. 1978 (most in 1977) as follows (number of collections in parentheses): Devils Gulch (1); Redstone site 1-5 (12); Redstone LS (2); Redstone NB (5); Redstone SB (3); Soldier Canyon (7).

Diagnosis. A medium-sized groundwater species, similar to *S. arizonensis* but distinguished by inner plate of maxilliped with plumose setae extending partway down inner margin, gnathopodal propod 1 with more oblique palm; 1 or 2 fewer teeth on palmar margin; distoposterior lobes of pereopod 6 and 7 better developed; telson shorter with a shallower notch and more spines on apical lobes (see Ward 1977; Ward and Holsinger 1981 for details). Largest ♀ 5.7 mm; largest ♂ 5.4 mm.

Distribution and ecology. This species is recorded from seeps, springs and interrupted stream drainage in the vicinity of Horsetooth Reservoir in Larimer Co., Colorado (see Ward and Holsinger 1981 for further details).

Stygobromus arizonensis Holsinger, 1974

Stygobromus arizonensis Holsinger, 1974: 47-49, figs. 28-29 [type-locality: small cave on Flying "H" Ranch near Fort Huachuca, Cochise Co., Arizona].

Material examined. ARIZONA. Cochise Co.: Mine Cave, south of Sierra Vista, 2 ♀♀, R. B. Pape, 17 Sept. 1994; Santa Cruz Co.: bog springs, Madera Canyon, 2 ♂♂, 1 juv., W. D. Sheppard, 3 June 1993.

Diagnosis. A relatively small to medium-sized cavernicolous species, distinguished by the diagnosis and description of Holsinger (1974). Largest ♀ 7.0 mm; largest ♂ 5.0 mm.

Distribution and ecology. This species is recorded from 4 localities (2 caves, 1 mine and 1 spring) in southeastern Arizona. Mine Cave is a natural cave that was broken into by miners and is located on the opposite side of Huachuca Mountains from the type-locality cave on Flying "H" Ranch (R. B. Pape, pers. comm.). The specimens from this cave were collected from a pool approximately 1.8 m deep and 61 m from the entrance. Bog spring is a spring/seep located approximately 48 km NNW of Fort Huachuca.

Stygobromus quatsinensis Holsinger and Shaw, 1987

Stygobromus n. sp. Holsinger and Shaw, 1986: 79.
Stygobromus quatsinensis Holsinger and Shaw, 1987: 222-229, figs. 1-3 [type-locality: Thanksgiving Cave, Vancouver Island, British Columbia, Canada]; Holsinger et al. 1997: 347-348.

Diagnosis. A medium-sized groundwater species, distinguished from most other members of the *hubbsi* group by presence of 2 or 3 submarginal setae on distal part of posterior margin of propod of gnathopod 1, inserted below defining angle; and absence of distal peduncular process on uropod 1 of male. Largest ♀ 9.0 mm; largest ♂ 7.0 mm.

Distribution and ecology. This species was originally described from two cave populations on Vancouver Island, British Columbia, Canada (Holsinger and Shaw 1986, 1987). Subsequently, the species has been found in caves elsewhere on Vancouver Island and in karst groundwater habitats (caves and resurgences) on several islands in the Alexander Archipelago of southeastern Alaska (Holsinger et al. 1997). Ovigerous females (6.0 -7.0 mm) occurred in two July samples from Alaska.

***Stygobromus wahkeenensis*, new species**
(Figs. 22, 23)

Stygobromus sp.— Bousfield and Holsinger, 1989: 968.

Material examined. OREGON. Multnomah Co.: railroad bank spring, Wakkeena Creek in Columbia River gorge, (elev. 183 m), HOLOTYPE ♀ (on slide mounts in part) (USNM 1000075), R. W. Wisseman, 17 Mar. 1989; seep or hyporheic habitat associated with Wahkeena Creek, ca. 3.1 km SSW of Bonneville, 3 ♀♀ paratypes, 2 juvs. (CMNC 2001-0023), G. W. Courtney, 19 Apr. 1985, 1 ♀, 1 ♂ (CMNC 2001-0024), 6 Mar. 1986.

Diagnosis. A small groundwater species distinguished as follows: palm of gnathopod 2 straight or slightly concave medially and with few teeth on palmar margin; maxilliped with bladelike spine on outer plate; bases of pereopods 5-7 rather narrow; pleonal plates 2-3 with 3 ventral spines each; uropod 1-2 moderately spinose; and telson longer than broad. Largest ♀, 4.0 mm, largest ♂, 3.0 mm.

Female. Antenna 1: 50 percent length of body, 46 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 4 plumose spines; palp segment 2 with row of 4 long setae on inner margin; palp segment 3 with 6 D setae and 4 E setae, lacking A, B and C setae. Inner lobes of lower lip absent. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 4 plumose spines, and 3 naked setae apically, and 1 plumose spine on inner margin; outer plate with setae on inner margin and apex, and small bladelike spine on or near apex.

Gnathopod 1: propod 1 subequal in size to that of gnathopod 2 but of different shape; palm straight or slightly concave and approximately 65 percent longer than posterior margin, armed with 16 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin without setae; 4 superior medial setae; 4-5 inferior medial setae; dactyl nail short; coxa about 2 times broader than deep, margin with 1 seta. Gnathopod 2: propod longer than broad; palm straight or slightly

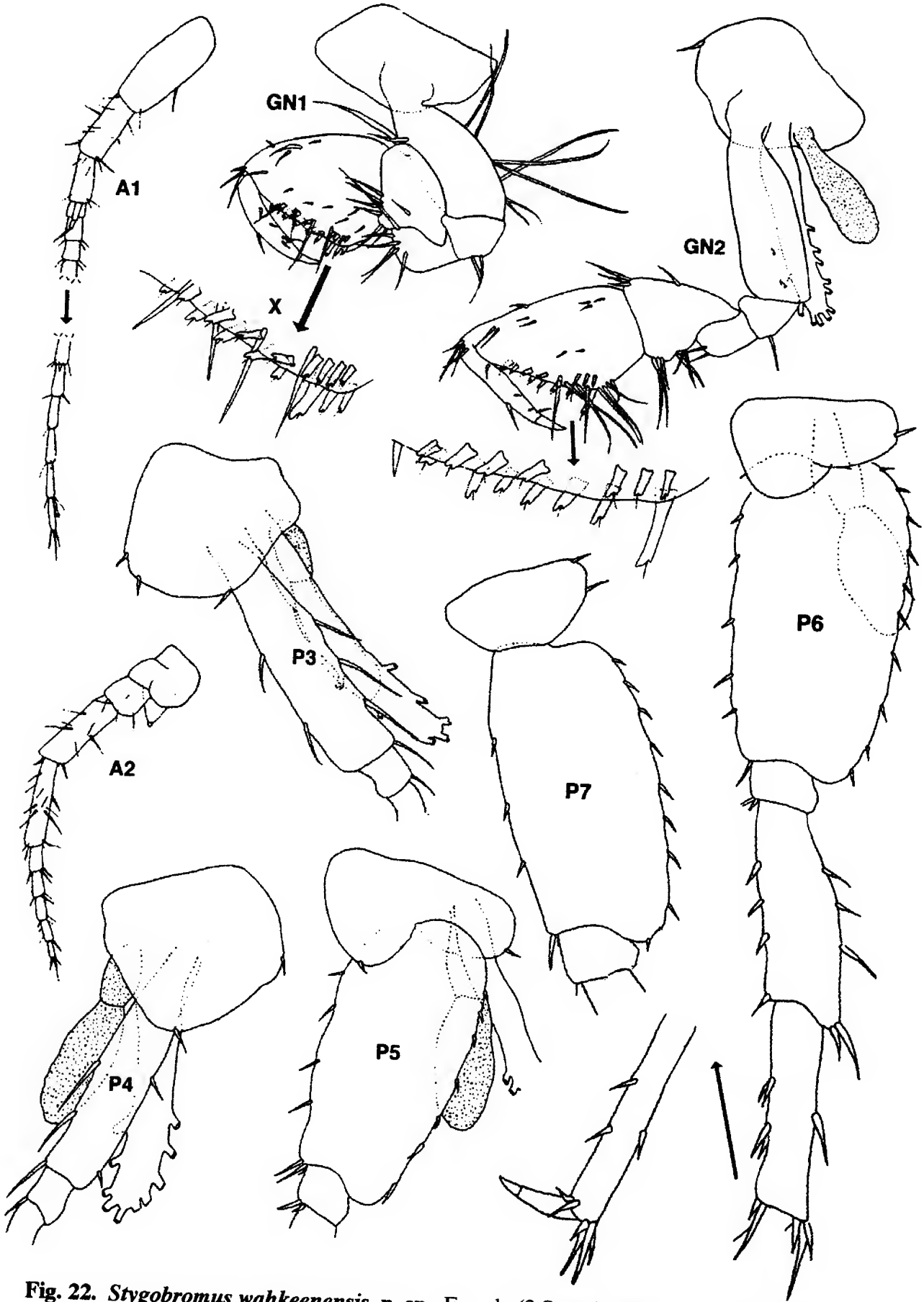

Fig. 22. ***Stygobromus wahkeenensis*, n. sp.** Female (3.8 mm). Multnomah County, Oregon.

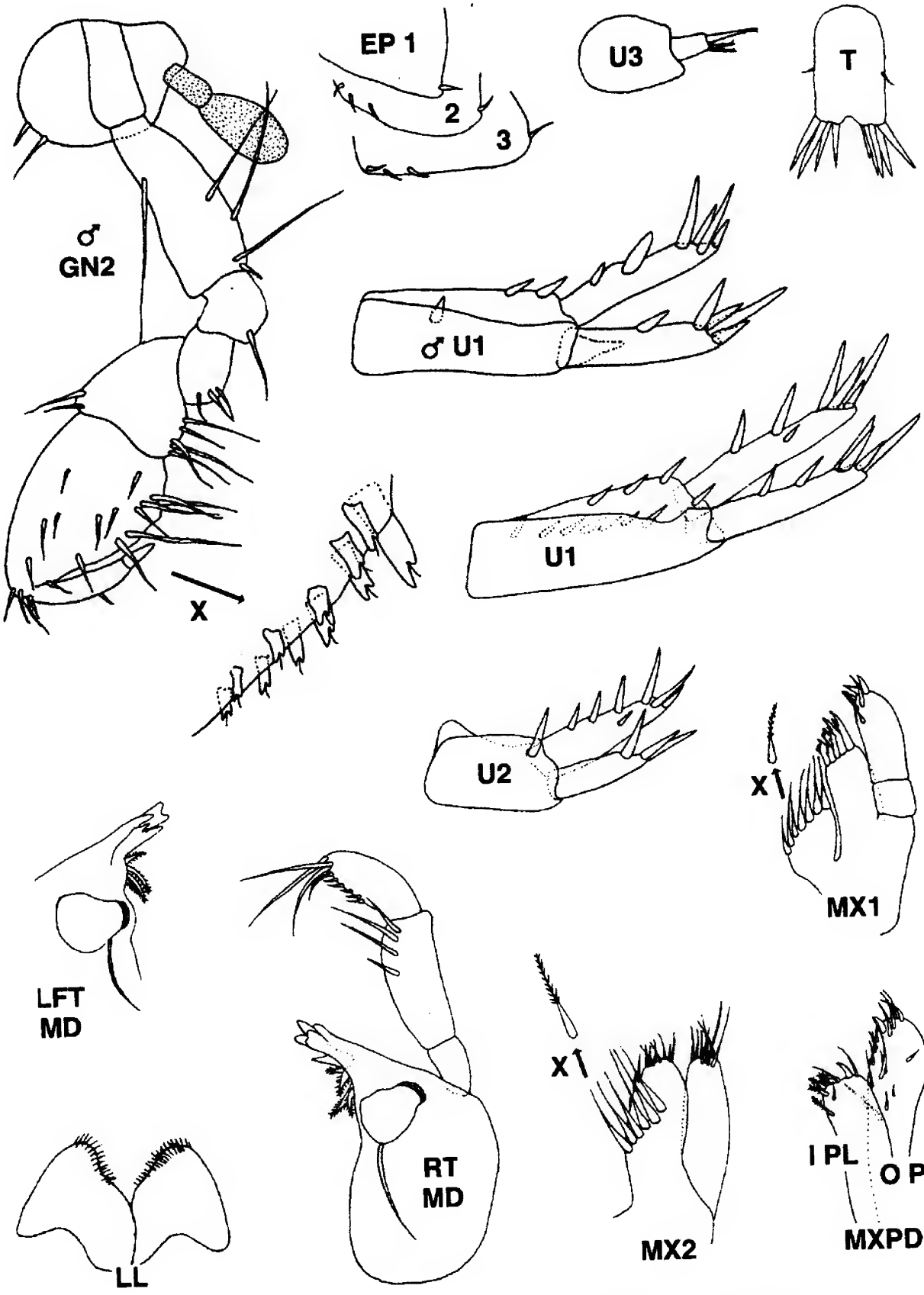

Fig. 23. ***Stygobromus wahkeenensis*, n. sp.** Female (3.8 mm); male (3.0 mm). Multnomah County, Oregon.

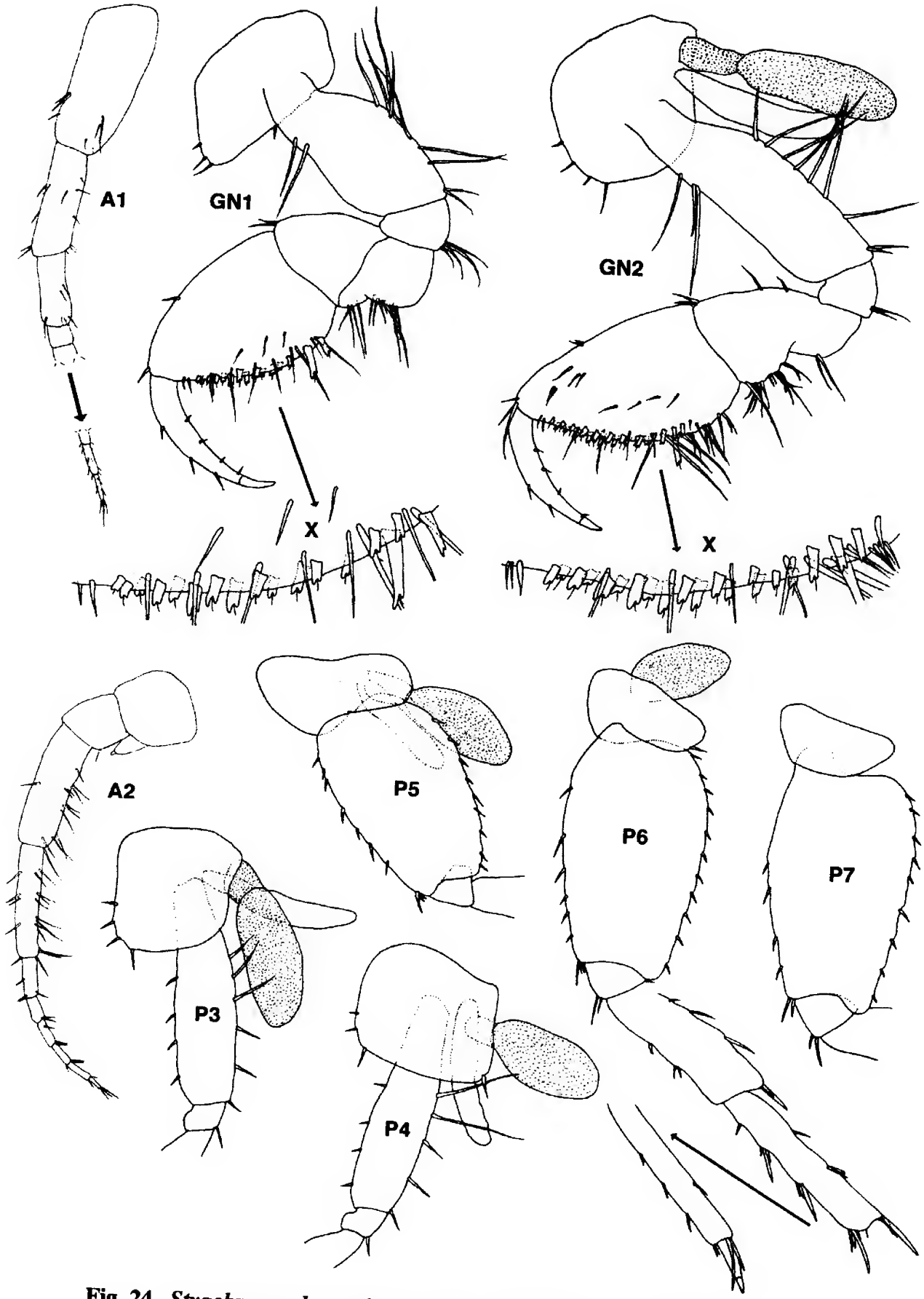

Fig. 24. ***Stygobromus lanensis*, n. sp.** Female (9.0 mm). Lane County, Oregon.

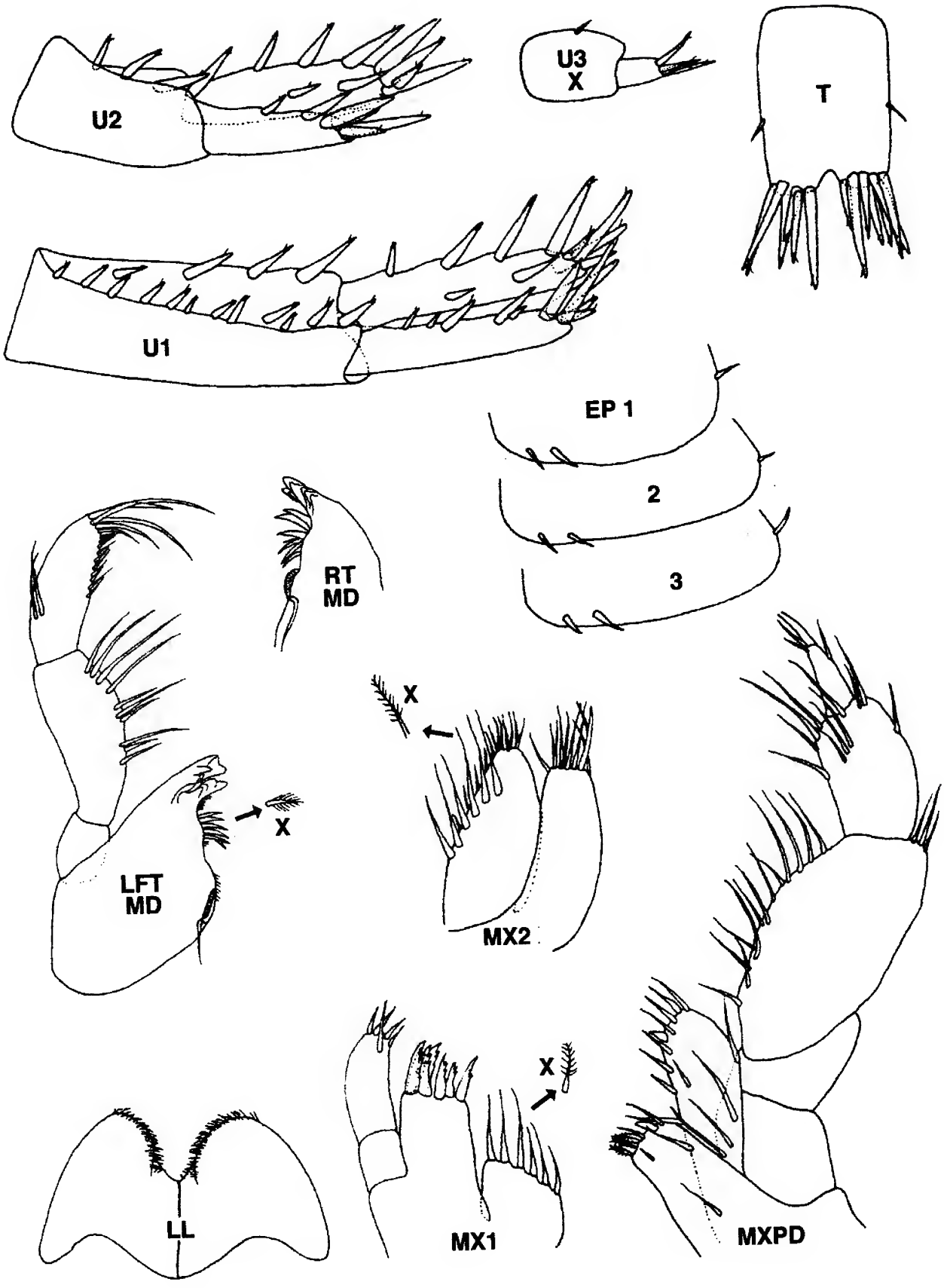

Fig. 25. ***Stygobromus lanensis*****, n. sp.** Female (9.0 mm). Lane County, Oregon.

concave medially and armed with 14 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin 30 percent length of palm, with 2 sets of doubly inserted setae; 6-7 doubly inserted superior medial setae; 2 inferior medial setae; coxa broader than deep, margin with 1 seta.

Pereopod 3: coxal plate about as broad as deep, margin with 3 setae. Pereopod 4: coxal plate little broader than deep, reaching about 30 percent length of basis, margin with 2 setae. Pereopod 6 little longer than pereopod 7, about 60 percent length of body, 40 percent longer than pereopod 5. Pereopods 5-7: bases about as broad proximally as distally; posterior margins weakly convex; distoposterior lobes well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 approximately 35 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates sublinear or slightly narrowing distally.

Pleonal plates: posterior margins of plate 1 - 3 straight or slightly convex, with 1 setule each near distoposterior corner; distoposterior corners rounded and that of plate 3 indistinct; ventral margin of plates 2 and 3 each with 3 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 45 percent length of peduncle, with 7 spines; outer ramus with 6 spines; peduncle with 11 spines. Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 7 spines; outer ramus with 3 spines; peduncle with 1 spine. Uropod 3: peduncle usually bearing 1 or 2 small setae; ramus approximately 45 percent length of peduncle, with 3 apical spines.

Telson subrectangular, longer than broad, apex with tiny median notch between spine clusters, bearing 9-10 relatively long spines.

Male. Differing from female as follows: gnathopod propods broader, palm of propod 2 shorter in relation to posterior margin, with fewer teeth on palmar margin. Uropod 1: peduncular process 30 percent length of outer ramus, narrowing distally, upper margin minutely serrate; inner ramus with 6 spines; peduncle with 3 spines. Uropod 2: inner ramus with 6 spines, peduncle with 2 spines. Telson with 10-12 apical spines.

Distribution and ecology. This species is recorded from the type-locality spring and a nearby seep and/or hyporheic zone associated with Wahkeena Creek in Multnomah Co., Oregon. The collections of March 1986 and 1989 also contained 18 and 9 specimens of *Stygonyx courtneyi* Bousfield and Holsinger (see Bousfield and Holsinger 1989).

Etymology. The epithet *wahkeenensis* is in reference to the association of this species with Wahkeena Creek.

Stygobromus lanensis, new species
(Figs. 24, 25)

Material examined. OREGON. Lane Co.: phreatic water habitat at H. J. Experimental Forest near Blue River Reservoir, HOLOTYPE ♀ (on slide mounts in part) (USNM 1000065), S. Wondzell, 3 July1991; hyporheic/seep area, Trail Creek, Willamette National Forest, 1 ♀ and 1 ♂ paratypes, 1 juv. (CMNC 2001-0022), G. W. Courtney, 22 May 1987.

Diagnosis. A medium-sized groundwater species, similar to *S. arizonensis* but distinguished as follows: posterior margin of gnathopod 1 shorter; distoposterior lobes of pereopod 6 distinct; pleonal plate 3 with 1 setule on posterior margin and 2 spines on ventral margin; uropods 1 and 2 with more long spines on rami and peduncles; and telson with more apical spines and only slight apical notch. Largest ♀, 9.0 mm; largest ♂ (?) 5.0 mm.

Female. Antenna 1: 56 percent length of body, 80 percent longer than antenna 2; primary flagellum with 20 segments. Antenna 2: flagellum with 6 segments.

Mandibles: spine row with 6-7 plumose spines; palp segment 2 with row of 10 setae on inner margin; palp segment 3 bearing 2 B setae, 9 D setae, and 5 E setae, lacking A and C setae. Inner lobes of lower lip vestigial. Maxilla 1: inner plate with 6 apical, plumose setae; palp with 5 stiff setae apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 3 plumose spines, and 2 naked setae apically, lacking plumose spines or coarse setae on inner margin; outer plate with few setae on inner margin and 4 setae and 1 bladelike spine on or near apex.

Gnathopod 1: propod slightly shorter than that of gnathopod 2; palm slightly convex and approximately 3 times longer than posterior margin, armed with 17 spine teeth in double row; defining angle with 1 spine tooth on outside, 1 shorter one on inside; posterior margin lacking setae; 1-2 superior medial setae and 3 inferior medial setae; dactyl nail short, all singly in-

serted; coxa about 2 times broader than deep, margin with 4 setae. Gnathopod 2: propod deeper than broad; palm convex medially and armed with 21-22 spine teeth in double row; defining angle with 1 long spine tooth on outside, 3 shorter spine teeth on inside; posterior margin approximately 50 percent length of palm, with 3 sets of setae; 5 superior medial setae, doubly inserted; 4 inferior medial setae; coxa deeper than broad, margin with 4 setae.

Pereopod 3: coxal plate about as deep as broad, margin with 4 setae. Pereopod 4: coxal plate little deeper than broad, reaching about 35 percent length of basis, margin with 4 setae. Pereopod 6 little longer than pereopod 7, about 60 percent length of body, 50 percent longer than pereopod 5. Pereopods 5-7: bases broader proximally than distally; posterior margins nearly straight; distoposterior lobes poorly developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 not particularly elongate, that of pereopod 6 about 30 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from pereopod 7. Brood plates slightly narrowing distally.

Pleonal plates: posterior margins of plates 1-3 convex, each with 1 setule near distoposterior corner, distoposterior corners rounded and indistinct; ventral margins of plates 1, 2 and 3 each with 2 spines. Uronites free. Uropod 1: inner ramus slightly longer than outer ramus, about 80 percent length of peduncle, with 10-11 spines; outer ramus with 10 spines; peduncle with 16 spines. Uropod 2: inner ramus longer than outer ramus, longer than peduncle, with 7 spines; outer ramus with 6 spines; peduncle with 4 spines. Uropod 3: peduncle usually bearing 1 small setae; ramus approximately 45 percent length of peduncle, with 4 apical spines.

Telson subrectangular, longer than broad; apical margin with tiny median notch between spine clusters, bearing 12-13 relatively long spines.

Distribution and ecology. This species is only known from its type-locality, where it was discovered by pumping from a cobble/gravel fill at a depth of 50-100 cm.

Etymology. This species is named for Lane County, Oregon.

Stygobromus sierrensis Holsinger, 1974

Stygobromus sierrensis Holsinger, 1974: 35-37, figs. 20-21 [type-locality: an unnamed spring in Trosi Canyon, Sierra Co., California].

Diagnosis. A medium-sized groundwater species and distinguished by shallow coxal plates of gnathopod 2 and pereopods 3 and 4; 2 ventral spines each on pleonal plates; proportionately short ramus of uropod 3; and near absence of apical notch of telson. Largest ♀, 7.0 mm; largest ♂, 5.2 mm.

Distribution and ecology. This species is known only from its type-locality.

Stygobromus putealis Holmes, 1909

Stygobromusputealis Holmes, 1909: 77-78, figs. [type-locality: well at Waupun, Dodge Co., Wisconsin.

Diagnosis. A medium-sized groundwater species, morphologically closely similar to many members of the *hubbsi* group much farther west. This species lacks sternal processes and setae on the posterior margin of the propod of gnathopod 1. Largest ♀, 6.0 mm; largest ♂, 4.0 mm.

Distribution and ecology. To date, all collections of this species have been from wells in southeastern Wisconsin, approximately 56 km east of the "Driftless Area." It is the only species of the *hubbsi* group found in central North America east of the western Cordillera.

Remarks: A detailed redescription of this species is being prepared by Holsinger (ms.).

Stygobromus lacicolus Holsinger, 1974

Stygobromus lacicolus Holsinger, 1974: 44-47, figs. 26-27 [type-locality: Lake Tahoe at Cave Rock, Douglas Co., Nevada].

Diagnosis. A medium-sized, deep-lake dwelling, stygomorphic species, that occurs sympatrically with *S. tahoensis* but is distinguished from that species by longer palms and more spines on gnathopodal propods; deeper coxal plates of pereopods 3 and 4, broader bases of pereopods 5-7; fewer spines on uropods 1 and 2; and longer ramus of uropod 3. Largest ♀, 6.0 mm; largest ♂, 5.5 mm.

Distribution and ecology. This species is only known from samples taken from Lake Tahoe. It is recorded

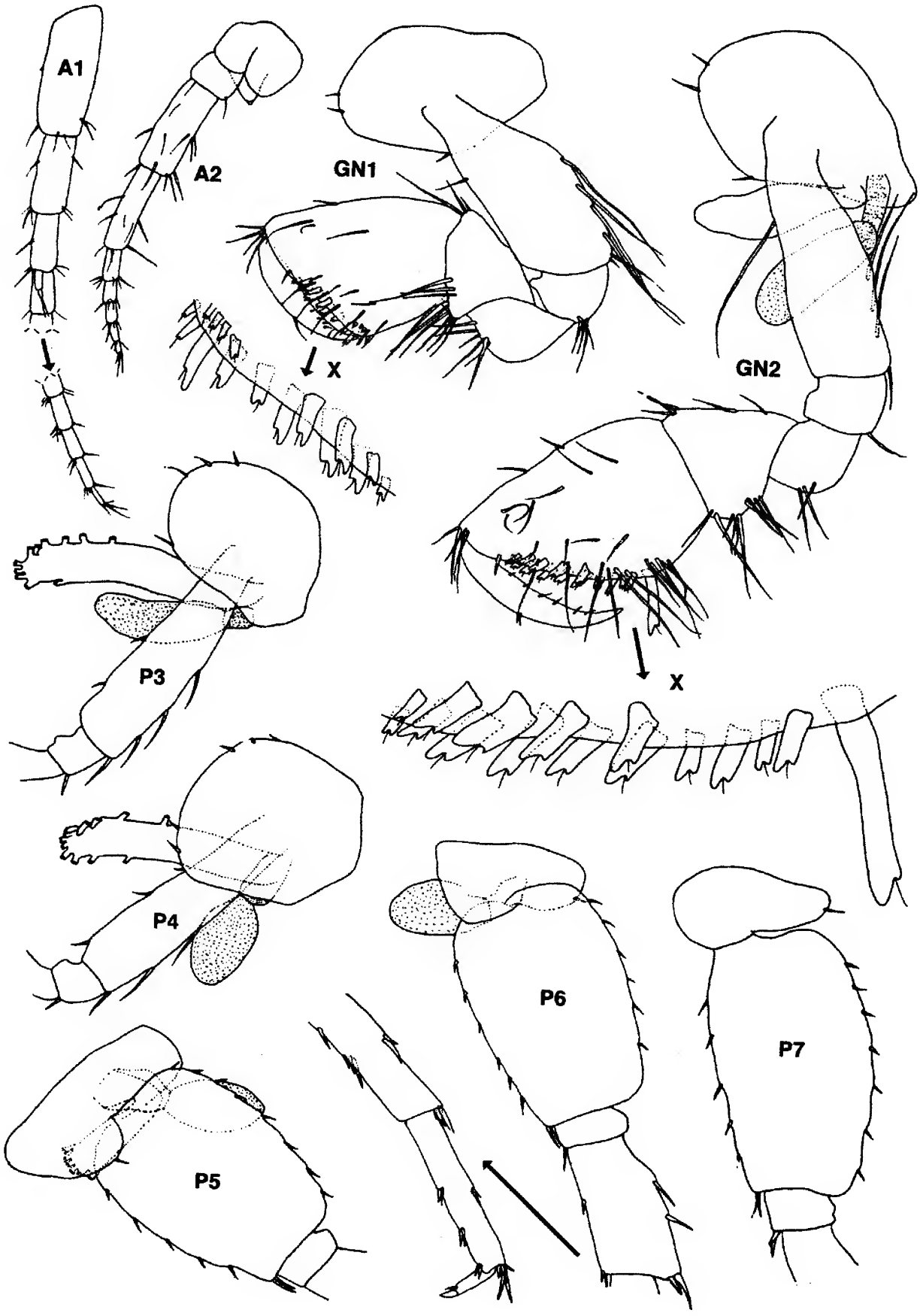

Fig. 26. ***Stygobromus myersae*, n. sp.** Female (5.0 mm). Inyo County, California.

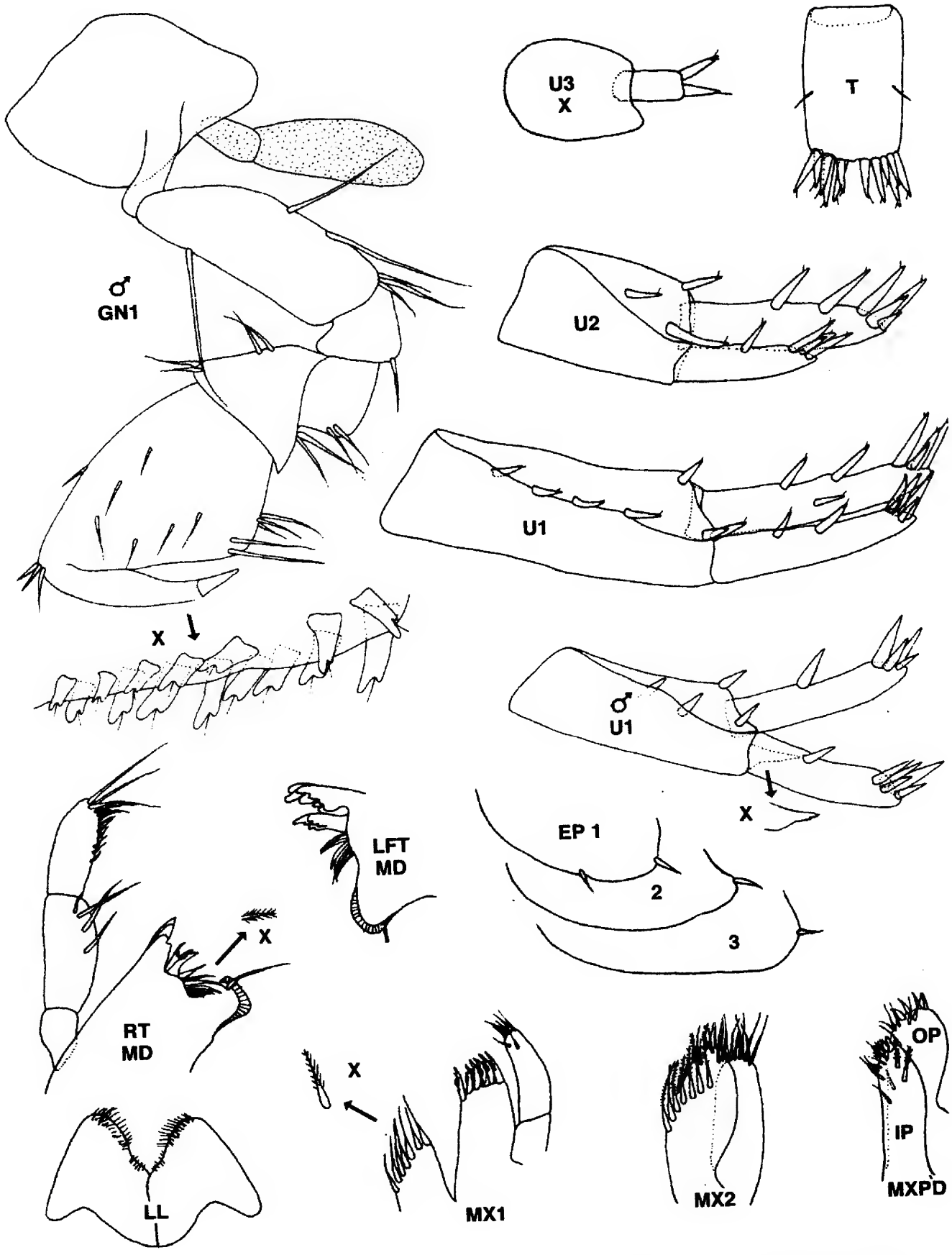

Fig. 27. ***Stygobromus myersae*****, n. sp.** Female (5.0 mm); male (3.8 mm). Inyo County, California.

from various sites in Lake Tahoe in El Dorado and Placer Cos., California and Douglas Co., Nevada (see Holsinger 1974).

Stygobromus sheldoni Holsinger, 1974

Stygobromus sheldoni Holsinger, 1974: 37-40, figs. 22-23 [type-locality: bog spring (elevation 1,920 m) tributary to Sagehen Creek, Nevada Co., California].

Material examined. CALIFORNIA. Nevada Co.: outflow pipe from boxed spring, Sagehen Field Research Station, north of Truckee, 1 ♂, 1 ♀, C. B. Barr and W. D. Shepard, 24-26 Sept. 1999.

Diagnosis. A small to medium-sized groundwater species probably closely related to both S. mackensiei and *S. sierrensis*. It differs from the latter by smaller size at sexual maturity, fewer spine teeth on palms of propod of gnathopod 1 of both sexes, proportionately smaller gnathopod propod 2 of male, and proximally broader bases of pereopods 5-7. Largest ♀, 5.5 mm; largest ♂, 4.8 mm.

Distribution and ecology. This species is recorded from a series of springs situated at elevations between 1915 and 2340 m (above sea level) that feed Segehen Creek in Nevada Co., California (see Holsinger 1974).

Remarks. In the recent (1999) sample by Barr and Shepard, both the male and female are at least 1.5 mm longer than any of the specimens described by Holsinger (1974) and differ slightly from the previously reported material as follows. The larger female has 3, instead of 2, apical spines on the ramus of uropod 3; and 12, instead of 10, apical spines on the telson. The larger male has a few more spine teeth on the gnathopod propods and 2-4 more apical spines on the telson.

Stygobromus myersae, new species
(Figs. 26, 27)

Material examined. CALIFORNIA. Inyo Co.: Black Canyon Spring, ca. 11 km E of Bishop, HOLOTYPE ♀ (USNM 1000068), 10 ♂♂ and 11 ♀♀ paratypes, 1 juv., M. Myers, 17 July 1997; 2 ♂♂, 6 ♀♀, 3 juvs., M. Myers, 4 Aug. 1996; unnamed hillside spring, ca. 7 km S of Black Canyon Spring, 5 juvs., M. Myers, 29 July 1998; 7 juvs., unnamed hillside spring in Marble Canyon, ca. 7 km S of Black Canyon Spring, 3 Nov. 1998; NEVADA. Esmeralda Co.: Log Spring, ca. 64 km E of Black Canyon Spring, 40 ♂♂ , 19 ♀♀, M. Myers, 30 Oct 1997.

Diagnosis. A medium-sized groundwater species distinguished as follows: propod of gnathopod 1 with relatively long posterior margin; propod of gnathopod 2 proportionately smaller; posterior margin of pleonal plates with few spines; and telson lacking apical notch. Largest ♀, 6.0 mm; largest ♂, 4.5 mm.

Female. Antenna 1: 46 percent length of body, 45 percent longer than antenna 2; primary flagellum with 10 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 6-7 plumose spines; palp segment 2 with row of 4 rather long setae on inner margin; palp segment 3 with 8 D setae, 4 E setae, lacking A, B and C setae. Inner lobes of lower lip vestigial or absent. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 7 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 7 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 3 plumose spines, 3-4 naked setae apically, and 2 plumose spines on inner margin; outer plate with setae on inner margin and setae and 1 or 2 small spines on apex.

Gnathopod 1: propod little smaller than propod of gnathopod 2; palm straight or slightly convex, and subequal in length to posterior margin, armed with 16 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin lacking setae; 3 superior medial setae, 4 singly inserted inferior medial setae; dactyl nail rather short; coxa broader than deep, margin with 3 setae. Gnathopod 2: propod relatively small, longer than broad; palm straight and armed with 16 spine teeth in double row; defining angle with 1 very long spine tooth of unequal length on outside, 1 shorter spine tooth on inside; posterior margin 50 percent length of palm, with 1 set of mostly doubly inserted (occasionally triply) setae; 6 doubly inserted superior medial setae, 4 singly inserted inferior medial setae; coxa about as broad as deep, margin with 3 setae.

Pereopod 3: coxal plate little deeper than broad, margin with 4 setae. Pereopod 4: coxal plate about as deep as broad, reaching about 40 percent length of basis, margin with 6 setae. Pereopod 6 little longer than pereopod 7, about 62 percent length of body, 33 percent longer than pereopod 5. Pereopods 5-7: bases about as broad proximally as distally; posterior margins convex; distoposterior lobes well developed, broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of

sponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates little expanded distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner, those of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 2 without spines, that of plate 3 with 1 spine. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 90 percent length of peduncle, with 7 spines; outer ramus with 7 spines; peduncle with 7 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 6 spines; outer ramus with 5 spines; peduncle with 3 spines. Uropod 3: peduncle usually without small setae; ramus approximately 55 percent length of peduncle, with 2 apical spines.

Telson subrectangular, longer than broad; apical margin typically entire, occasionally with tiny median notch or "break" between spine clusters, bearing 12 relatively long spines.

Male. Differing from female as follows: gnathopod propods proportionately shorter, palm of propod 2 slightly longer in relation to posterior margin and with fewer teeth on palmar margin. Uropod 1: peduncular process 33 percent length of outer ramus, sharply pointed distally, upper margin minutely serrate; inner ramus with 5 spines; peduncle with 4 spines. Uropod 2: inner ramus with 7 spines, peduncle with 4 spines. Telson with 12-14 apical spines.

Distribution and ecology. This species is recorded from two springs, approximately 7 km apart, in Inyo Co., California, and one spring in Esmeralda Co., Nevada, about 64 km to the east. Samples from Black Canyon Spring were obtained through a PVC pipe pushed into the substrate and with an aquarium net (M. Myers pers. comm.). The water temperature in the spring was about 10°C. Elsewhere, in the unnamed spring in Marble Canyon, the water temperature was about 12.8°C. Females ranging in size from 5.0 - 6.0 mm have setose brood plates and are sexually mature.

Etymology. This species is named in honor of its collector, Marilyn Myers, who collected several good samples of this species and furnished useful data on its ecology.

Stygobromus cherylae, new species
(Figs. 28, 29)

Material examined. CALIFORNIA. Sonoma Co.: unnamed spring box, just east of Maacama Creek Bridge, beside Highway 128, approximately 19.5 km east of Geyserville, HOLOTYPE ♀ (USNM 1000052), and 60 paratypes (EME and JRH), C. B. Barr and W. B. Shepard, 21 Feb. 2000; spring box and feeder pipe in the same location, 1 ♂, 1 juv., C. B. Barr, 5-7 Oct 1995; feeder pipe at spring box, 19.5 km east of Geyserville, 1 ♀, 2 juvs., 26-28 Apr. 1996; pipe at unnamed spring on hillside, 19.5 km east of Geyserville, ♀♀, 33 juvs., 26-28 Apr. 1996.

Diagnosis. A medium-sized groundwater species, probably closely related to the *S. grahami* species complex farther to the east, but characterized by smaller males at sexual maturity. Further distinguished from *S. grahami* by having fewer setae on inner plates of maxillae and maxilliped; nearly straight to slightly convex palms of propods of gnathopods 1 and 2; coxal plates 1 and 2 proportionately smaller; pleonal plates 2 and 3 with fewer ventral spines; apical margin of telson with tiny notch. Largest ♀, 7.5 mm; largest ♂, 4.5 mm.

Female. Antenna 1: 60 percent length of body, 24 percent longer than antenna 2; primary flagellum with 18 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 5-6 plumose spines; palp segment 2 with 6 long setae on inner margin, 2 on outer margin; palp segment 3 with 5 C setae, about 10 D setae and 5 E setae, lacking both A and B setae. Inner lobes of lower lip absent. Maxilla 1: inner plate with 8 apical plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 9 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 2 plumose spine, and 2 naked setae apically, and 2 coarse plumose setae on inner margin; outer plate with setae on inner margin and apex, and 1 bladelike spine on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm slightly convex or straight and approximately 2 times longer than posterior margin, armed with 22 spine teeth in double row; defining angle with 3 spine teeth on outside, 2 shorter ones on inside; posterior margin without setae; 4 doubly inserted superior medial setae; 4 or 5 inferior medial setae; dactyl nail short; coxa approximately 2 times broader than deep, margin with 3 setae. Gnathopod 2: propod deeper than broad; palm convex medially and armed with 21-22 spine teeth in double row; defining angle with 1 long spine tooth on outside, 1 shorter spine tooth on inside; posterior margin about 25 percent of length palm, with 2 sets of doubly or triply inserted setae; 9 - 10 doubly inserted superior medial setae; 4 or 5 singly inserted inferior medial setae; dactyl nail shorter; coxa broader than deep, margin with 4 setae.

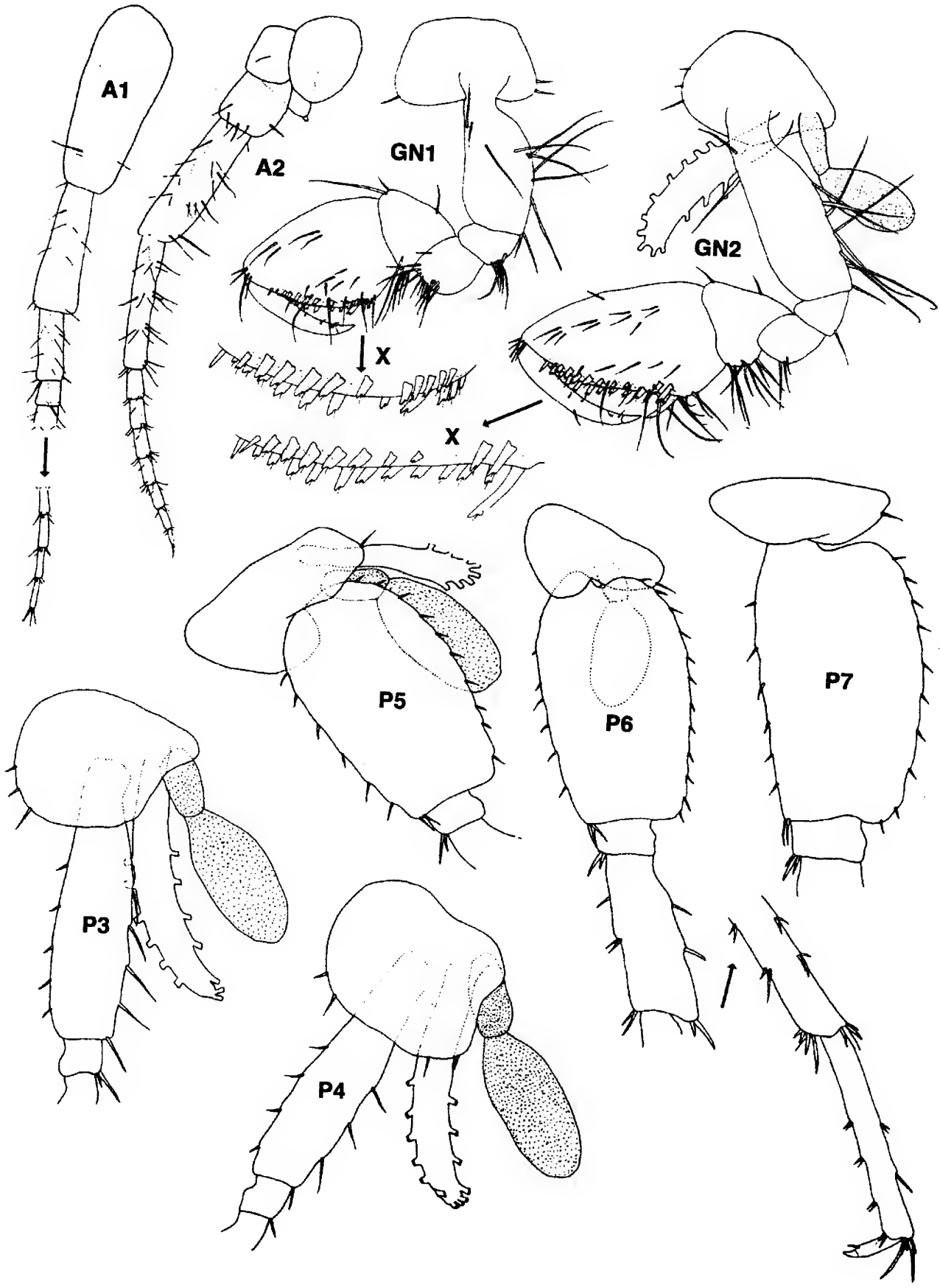

Fig. 28. ***Stygobromus cherylae*, n. sp.** Female (7.0 mm). Sonoma County, California.

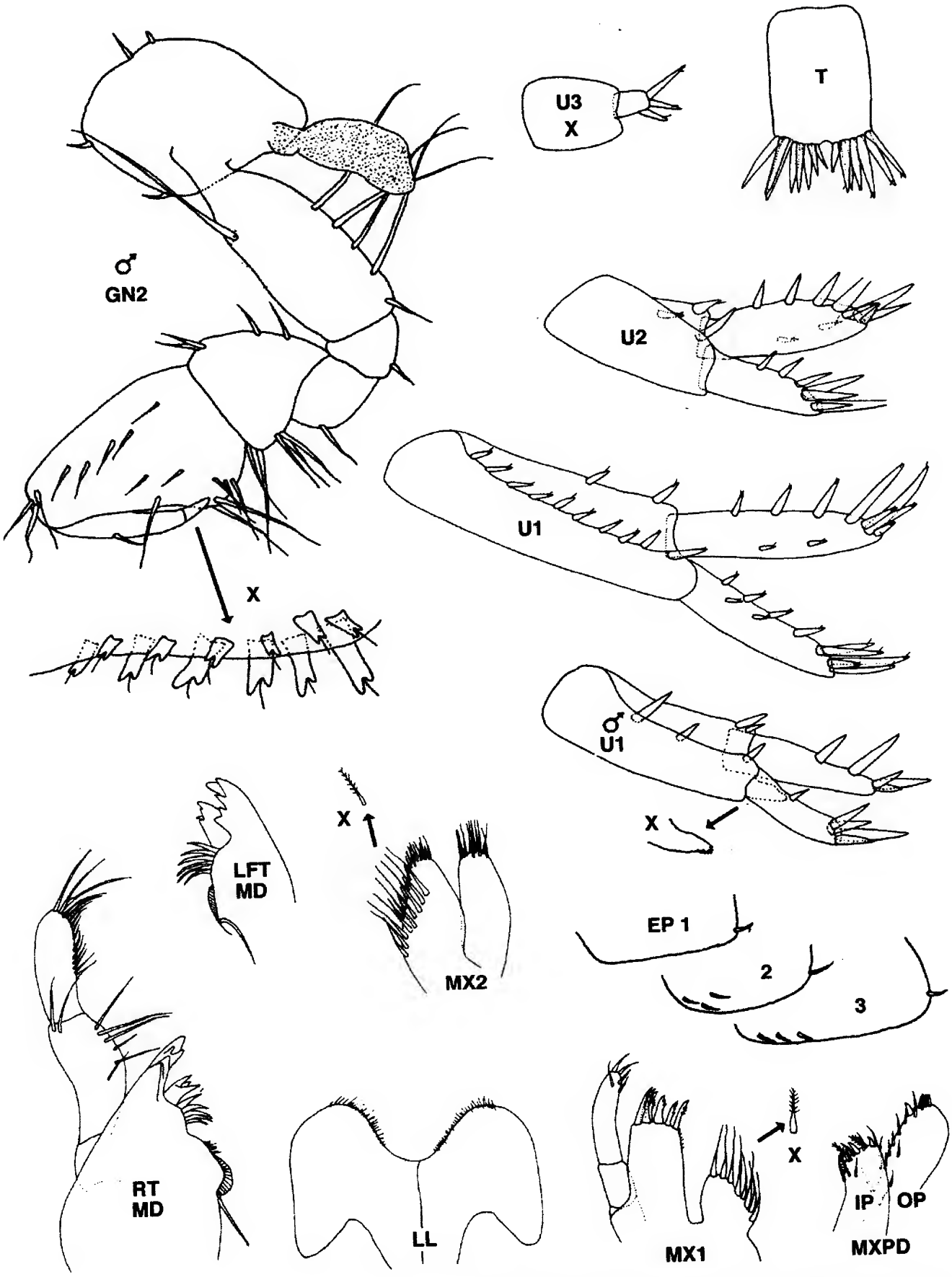

Fig. 29. ***Stygobromus cherylae*, n. sp.** Female (7.0 mm); male (4.5 mm). Sonoma Co., California.

Pereopod 3: coxal plate about as broad as deep, margin with 3 setae. Pereopod 4: coxal plate about as broad as deep, reaching about 33 percent length of basis, margin with 4 setae. Pereopod 6, slightly longer than pereopod 7, about 57 percent length of body, 33 percent longer than pereopod 5. Pereopods 5-7: bases as broad proximally as distally; posterior margins variably convex; distoposterior lobes moderatedly well developed, anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 approximately 30 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from pereopod 7. Brood plates slightly narrowing distally.

Pleonal plates: posterior margin of plate 3 convex, with 1 setule near distoposterior corner, that of plates 1 and 2 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plates 2 and 3 each bearing 3 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 75 percent length of peduncle, with 10 spines; outer ramus with 11 spines; peduncle with 12 spines. Uropod 2: inner ramus longer than outer ramus, longer than peduncle, with 10 spines; outer ramus with 7 spines; peduncle with 3 spines. Uropod 3: peduncle not bearing setae; ramus approximately 30 percent length of peduncle, with 3-4 apical spines.

Telson longer than broad, apical margin with tiny median notch between spine clusters, bearing 14-16 relatively long spines.

Male. Differing from female in a number of characters as follows: sexually mature specimens approximately 3.0 mm shorter; antenna 1 with longer esthetascs, and presence of peduncular process on uropod 1, which is approximately 20-25 percent length of outer ramus. Gnathopod propods smaller, palm of propod 2 longer than posterior margin, with fewer teeth on palmar margin. Uropod 2: inner ramus with 9-11 spines, peduncle with 3-5 spines. Telson with 13-15 apical spines.

Distribution and ecology. This species is only known from its type-locality. According to C. B. Barr (pers. comm.), who collected most of the specimens, some of the water from the spring is diverted at the spring head into a feeder pipe that carries water downhill to a spring box. Specimens were obtained from both the feeder pipe (by netting) and spring box. The large 21 February collection was made by picking through roots and debris in the upper spring box.

Etymology. It is a pleasure to name this species for Cheryl B. Barr in recognition of her collections of amphipods from springs in western North America and for supplying our study with useful data on habitats and collecting techniques

Remarks. A second, smaller (undescribed) species of *Stygobromus,* occurs with *S. cherylae* in the type-locality, but was not detected until the collection of 21 February 2000 was examined. The second species, which is distinguished by significantly smaller size at sexual maturity, proportionately shorter appendages, broader bases of pereopods 6 and 7, and fewer spines on the uropods and telson, will be described in a subsequent paper.

Stygobromus cowani, new species
(Fig. 30)

Material examined. CALIFORNIA. Napa Co.: roadside pipe from unnamed spring, Soda Canyon Road, approximately 6.4 km north of junction with Silverado Trail and about 6.4 km east of Yountville, HOLOTYPE ♀ (on 2 slide mounts in part) (USNM 1000053), 1 ♂ (in poor shape), 1 juv., C. B. Barr, 23 Feb. 1991.

Diagnosis. A small groundwater species closely related to *S. gradyi* but distinguished as follows: maxilla 1 with 8-9 setae on inner plate; maxilla 2 and maxilliped with fewer setae on inner plate; lower lip without inner lobes; palm of propod of gnathopod 2 slightly concave; coxal plate of pereopods 3 and 4 deeper than broad; and ventral margin of pleonal plate 2 with fewer spines. Largest ♀, 4.6 mm; ♂ ca. 3.5 mm.

Female. Antenna 1: 52 percent length of body, 76 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 6-8 plumose spines; palp segment 2 with 5 long setae on inner margin; palp segment 3 with 5-6 C setae, 5 D setae, and 5 E setae, lacking both A and B setae. Inner lobes of lower lip vestigial or absent. Maxilla 1: inner plate with 9 apical plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 10 plumose setae on inner margin. Maxilliped: inner plate with 3 blade-like spines, 3 plumose spines and 1 naked seta apically on inner margin; outer plate with setae on inner margin and 10-12 lightly plumose setae on or near apex.

Gnathopod 1: propod shorter than that of gnathopod 2; palm straight or slightly concave medially, little

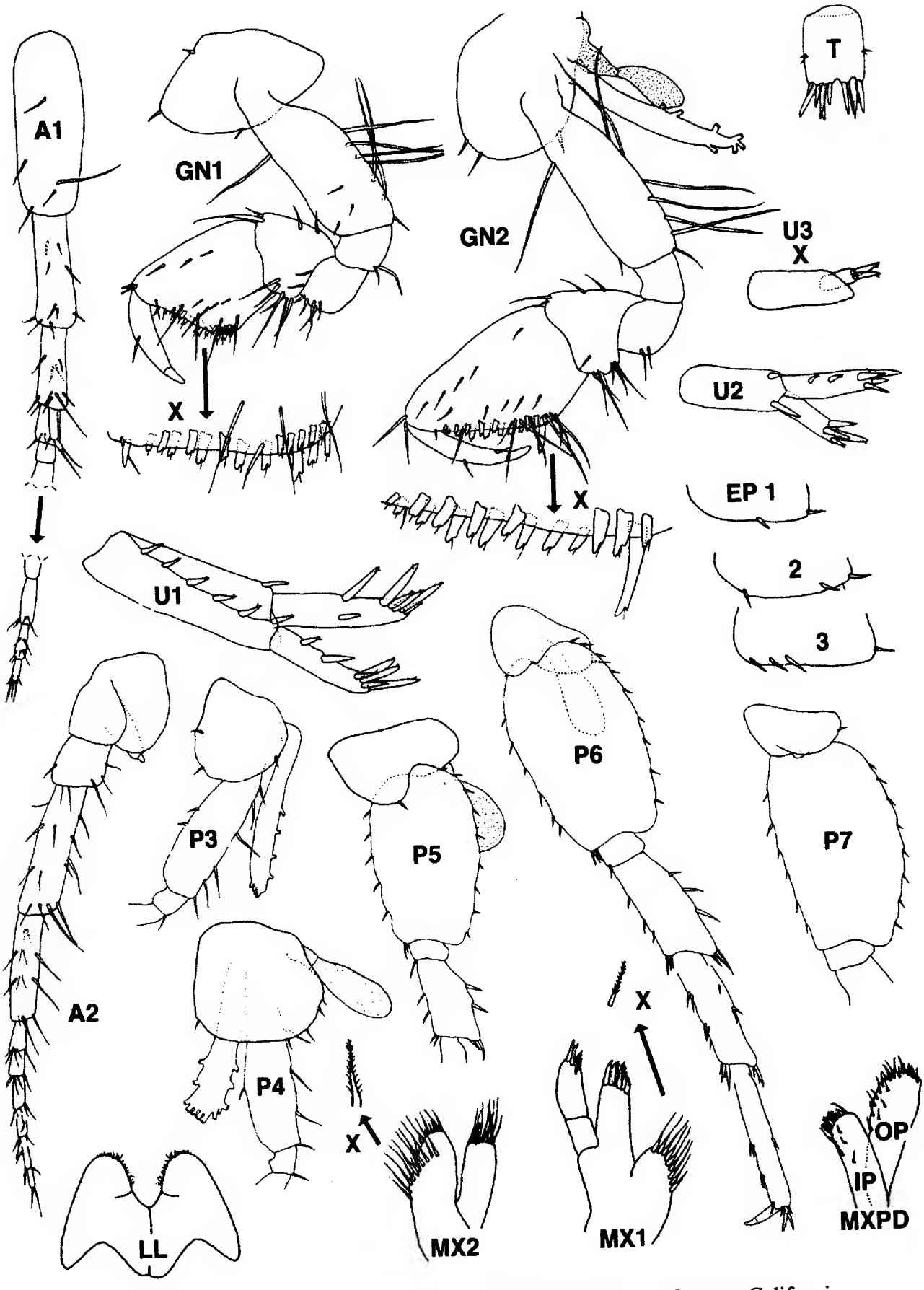

Fig. 30. *Stygobromus cowani*, n. sp. Female (4.6 mm). Napa County, California.

longer than posterior margin, armed with 16 spine teeth in double row; defining angle with 3 spine teeth on outside, 4 shorter ones on inside; posterior margin not bearing setae; 3 singly inserted superior medial setae; 4 singly inserted inferior medial setae; dactyl nail short; coxa about as broad as deep, margin with 3 setae. Gnathopod 2: propod longer than broad; palm straight or very weakly concave, and armed with 16 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin approximately 50 percent length of palm, with 1 set of triply inserted setae; 5 -6 singly inserted superior medial setae; 4 singly inserted inferior medial setae; coxa little deeper than broad, margin with 3 setae.

Pereopod 3: coxal plate about as deep as broad, margin with 3 setae. Pereopod 4: coxal plate relatively broad, broader than deep, reaching about 40 percent length of basis, margin with 5 setae. Pereopod 6 little longer than pereopod 7, about 44 percent length of body, 11 percent longer than pereopod 5 in length. Pereopods 5-7: bases broader proximally than distally; posterior margins convex but more strongly convex in pereopod 7; distoposterior lobes relatively well developed, broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender, that of pereopod 6 typically 33 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from pereopod 7. Brood plates sublinear, slightly broader distally.

Pleonal plates: posterior margin of plate 1 weakly convex, with 1 setule near distoposterior corner, that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded, indistinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 3 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, with 7 spines, about 75 percent length of peduncle; outer ramus with 7 spines; peduncle with 7 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 6 spines; outer ramus with 4 spines; peduncle with 2 spines. Uropod 3: peduncle narrow, lacking small setae; ramus also narrow, approximately 30 percent length of peduncle, with 2 apical spines.

Telson little longer than broad; apical margin with tiny median notch between spine clusters, with 11-12 relatively long spines.

Distribution and ecology. This species is only known from its type-locality. The type material is in poor shape. The male specimen is covered by fungi and can not be measured accurately or dissected.

Etymology. This species is named for David Cowan, in recognition of his able assistance with the collection of amphipods from subterranean waters in California.

Stygobromus tahoensis Holsinger, 1974

Stygobromus tahoensis Holsinger, 1974: 40-44, figs. 24-25 [type-locality: Lake Tahoe, at about 61 m depth, between Skunk Harbor and Tahoe City, Placer Co., California].

Material examined. CALIFORNIA.: Lake Tahoe in Chara bed at 61m depth, 15 ♀♀, 3 ♂♂ paratypes, E. R. Byron, fall 1979.

Diagnosis. A medium-sized, deep-lake dwelling, stygomorphic species, apparently related to *S. sierrensis* and *S. sheldoni*, but distinguished from these 2 species by the diagnosis and description of Holsinger (1974). Largest ♀, 6.5 mm; largest ♂, 5.0 mm.

Distribution and ecology. This species is known only from Lake Tahoe, where a majority of specimens were collected at depths of 60-495 m (see Holsinger 1974).

Stygobromus mackenziei Holsinger, 1974

Stygobromus mackenziei Holsinger, 1974: 32-35, figs. 18-19 [type-locality: Empire Cave, Santa Cruz Co., California].

Material examined. CALIFORNIA. Santa Cruz Co.: Empire Cave, 5 ♀, D. C. Rudolph, D. Cowan and B. van Ingen, 22 Apr. 1979; 2 ♀♀, T. S. Briggs, 4 Dec. 1983.

Diagnosis. A small cavernicolous species, distantly related to species of the Mother Lode region of California and distinguished by having 4 apical spines on inner plate of maxilliped: lightly spined palms of gnathopodal propods, relatively large, deep coxal plates of gnathopods and pereopods 3 and 4; proportionately broad bases of pereopods 5-7, lightly spined peduncles of uropods 1 and 2, and 8 apical spines on telson. Largest ♀, 6.0 mm; largest ♂, 4.0 mm.

Distribution and ecology. This species is known only from its type-locality. Several of the females in the

April 1979 sample measured 6.0 mm and had setose brood plates. One specimen was ovigerous with 7 embryos in the brood pouch. This collection also contained 1 specimen of *Stygobromus imperialis* n. sp. (described below). The December 1983 collection was taken from a flooded room with 2 specimens of *Calasellus californicus* (see Lewis 2001) and 2 stygobiont isopods of the genus *Caecidotea*.

Stygobromus oregonensis Holsinger, 1974

Stygobromus oregonensis Holsinger, 1974: 13-16, figs. 6-7 [type-locality: small unnamed cave near Roseburg, Douglas Co., Oregon].

Material examined. OREGON. Douglas Co.: a small cave near Roseburg (type-locality), 2 ♀♀ topotypes, Jim Riggs, 1 Jan. 1983.

Diagnosis. A moderately cavernicolous species easily distinguished from other species of the *hubbsi* group by numerous long, stiff setae and slender spines on peduncular segments 4 and 5 of antenna 2; proportionately large propod gnathopod 1 with very long, heavily spined palm; convex palm of gnathopodal propod 2 with double row of 16 spine teeth; convex posterior margins of bases of pereopods 5-7; midlateral position of posterior subacute distoposterior corners of pleonal plates 2 and 3; and larger ramus of uropod 3. Largest ♀, 13.0 mm; ♂, unknown.

Distribution and ecology. This species is known only from type-locality. Two samples, containing only females, have been collected from a pool in the bottom of the cave. According to Jim Riggs (pers. comm.), the cave is a single passage developed in the Eocene-aged Umpqua formation, which was formed by faulting and/or fissuring in sandstone or siltstone conglomerate. It is not developed in basalt as stated earlier by Holsinger (1974).

Stygobromus hubbsi Shoemaker, 1942

Stygobromus hubbsi Shoemaker, 1942: 1-6, figs. 1-2 [type-locality: Malheur Cave, Harney Co., Oregon]. See Holsinger (1974) for earlier synonymy.

Diagnosis. Corresponding to the redescription by Holsinger (1974). A medium-sized cavernicolous species, closely allied morphologically with species of *Stygobromus* from east-central California (especially *S. grahami, S. harai,* and *S. wengerorum)* but distinguished by having fewer plumose setae on inner plates on maxillae 1 and 2; fewer apical spines on inner plate of maxilliped; and fewer apical spines on apical margin of telson. Largest ♀, 6.5 mm; largest ♂, 5.5 mm.

Distribution and ecology. This species is known only from a lake in the type locality, Malheur Cave, Harney Co., Oregon. According to John Markham (pers. comm.), who is involved with a recent research project in the cave, amphipods are attracted to baited traps left in the cave lake. A recent map and description of Malheur Cave were given by Hill (2000).

Stygobromus mysticus Holsinger, 1974

Stygobromus mysticus Holsinger, 1974: 49-52, figs. 30-31 [type-locality: subterranean habitat, Greenview, Siskiyou Co., California].

Diagnosis. A medium-sized subterranean species, distinguished by possession of relatively small gnathopod propods; deep coxal plates; broadly expanded bases of pereopods 5-7; narrow outer rami of uropod 1 and 2; and long, distally tapering telson. Largest ♀, 8.0 mm; ♂, unknown.

Distribution and ecology. This species is known only from subterranean habitat, possibly from a well, in the Klamath Mountains, Siskiyou Co., California (Holsinger 1974).

Stygobromus hyporheicus, new species
(Figs. 31, 32)

Material examined. CALIFORNIA. Marin Co.: gravel-bed of intermittent stream, Cronan Creek, HOLOTYPE ♀ (USNM 1000060), ♀♀ paratypes, 2 juvs., R. Leach, 15 July 1997.

Diagnosis. A medium-sized interstitial species, similar to *S. grahami* and *S. wengerorum* but distinguished from those as follows: maxillae 1 and 2 with fewer setae on inner plates; palms of gnathopod 1 and 2 convex or straight, and with more spine rows; coxal plates 3 and 4 broader than deep; pleonal plates 2 and 3 with fewer ventral margin spines, but with more posterior margin spines; uropods 1-3 with more spines on peduncles and rami; telson 2 times deeper than broad. Largest ♀, 7.0 mm; ♂, unkown.

Female. Antenna 1: 70 percent length of body, 78 percent longer than antenna 2; primary flagellum with

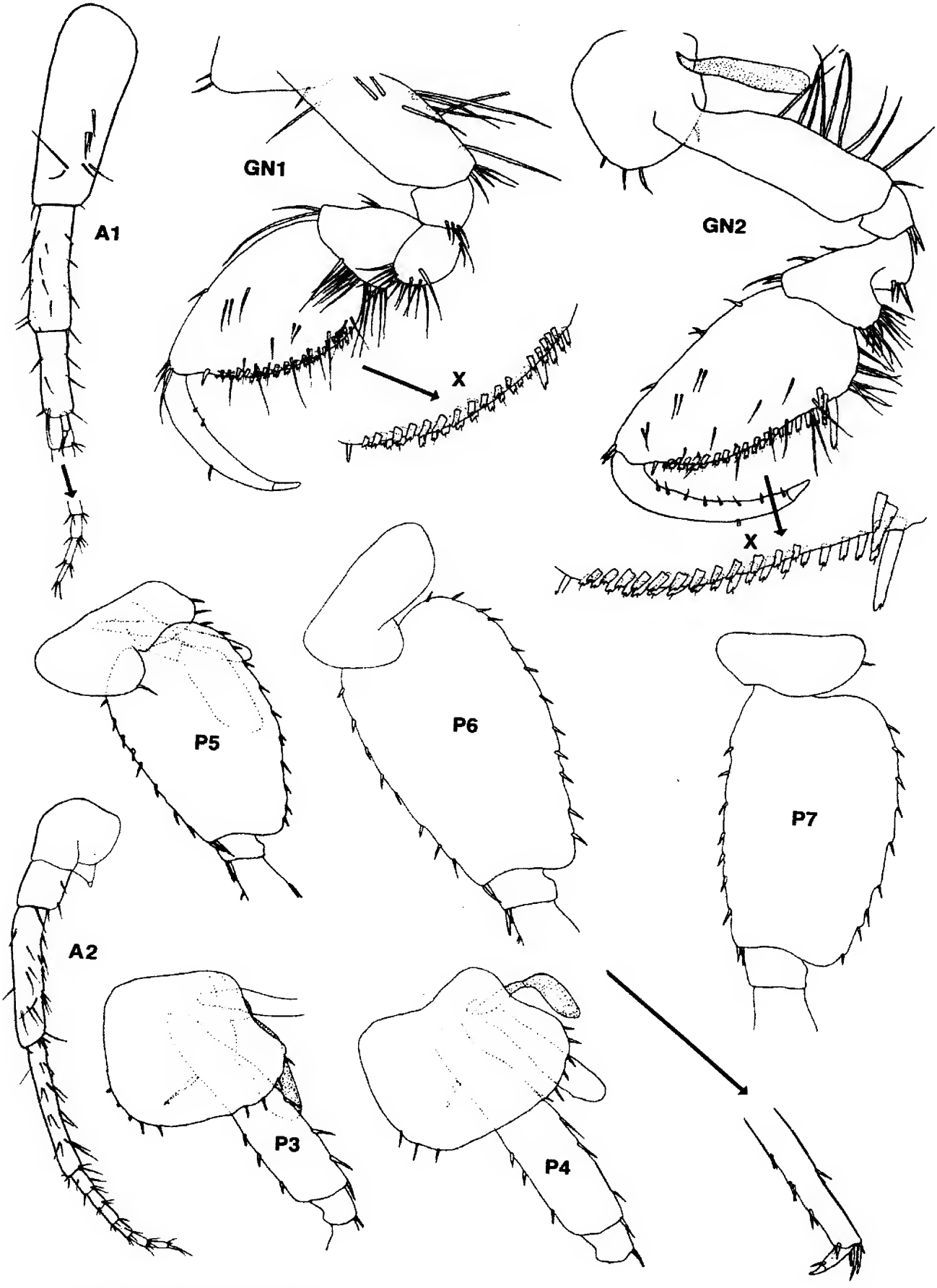

Fig. 31. ***Stygobromus hyporheicus*****, n. sp.** Female (7.0 mm). Marin County, California.

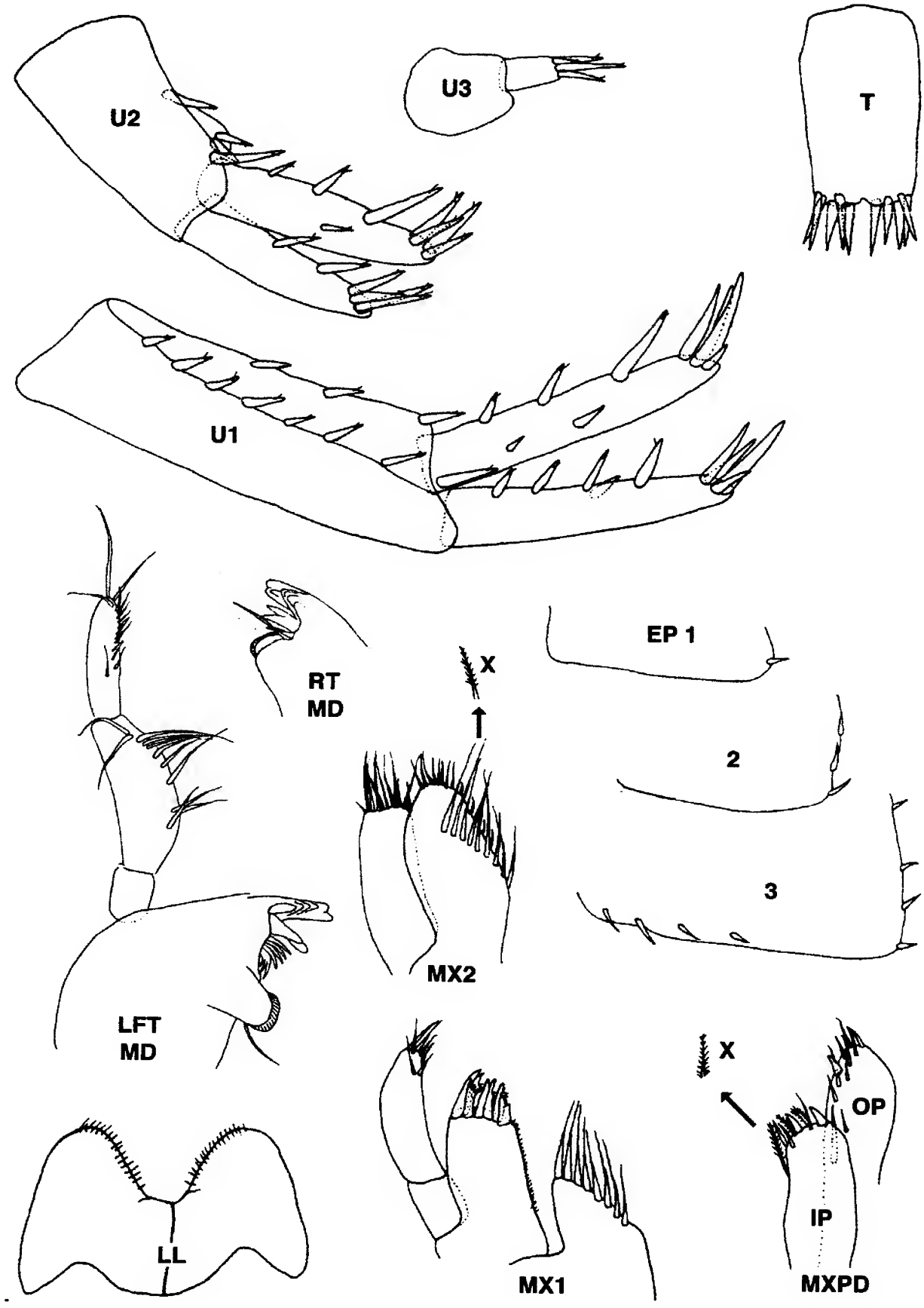

Fig. 32. ***Stygobromus hyporheicus*****, n. sp.** Female (7.0 mm). Marin County, California.

21 segments. Antenna 2: flagellum with 7 segments.

Mandibles: spine row with 7-8 plumose spines; palp segment 2 with row of 11 setae on inner margin, segment 3 bearing 3-4 C setae, approximately 8 D setae, 3 E setae, lacking A and B setae. Inner lobes of lower lip vestigial or absent. Maxilla 1: inner plate with 8 apical plumose setae; palp with 7 stiff setae or slender spines apically or subapically. Maxilla 2: inner plate with oblique row of 9 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 9 plumose spines, 2 naked setae apically and 1 plumose seta on inner margin; outer plate with few setae, 1 bladelike spine, and 8-9 lightly plumose setae on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight or slightly convex and about 67 percent longer than posterior margin, armed with 35 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin lacking setae; 3 superior medial setae; 3 -4 inferior medial setae; dactyl nail short; coxa broader than deep, margin with 3 setae. Gnathopod 2: propod deeper than broad; palm straight or slightly convex and armed with 34 spine teeth in double row; defining angle with 2 spine teeth of unequal length on outside, 2 shorter spine teeth on inside; posterior margin approximately 30 percent length of palm, with 2-3 sets of doubly inserted setae; 6 doubled inserted superior medial setae; 3 inferior medial setae, 2 medial setae; coxa slightly broader than deep, margin with 4 setae.

Pereopod 3: coxal plate broader than deep, margin with 8-9 setae. Pereopod 4: coxal plate broader than deep, reaching approximately 50 percent length of basis, margin with 8-9 setae. Pereopod 6 slightly longer than pereopod 7, about 70 percent length of body, 30 percent longer than pereopod 5. Pereopods 5-7: bases broader proximally than distally; posterior margins convex proximately; distoposterior lobes developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish spines; dactyls of pereopods 5-7 relatively elongate, that of pereopod 6 approximately 33 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from pereopod 7. Brood plates slightly narrowing distally.

Pleonal plates: posterior margin of plate 2 convex, with 4 setae, that of 1 and 3 less convex, plate 1 with 1 setule near distoposterior corner, plate 3 with 4 setules; distoposterior corners rounded; ventral margin of plates 1 and 2 without spines, that of plate 3 with 4 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 9-10 spines; outer ramus with 9 spines; peduncle with 10 spines. Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 8 spines; outer ramus with 7 spines; peduncle with 3 spines. Uropod 3: peduncle without setae; ramus approximately 33 percent length of peduncle, with 4 or 5 apical spines.

Telson much longer than broad, apical margin with small median notch between spine clusters, with 9-10 relatively long spines.

Distribution and ecology. This species is known from the hyporheic zone of a gravel-bedded intermittent stream, Cronan Creek, in Golden Gate National Recreational Area, which is adjacent to Point Reyes National Seashore. The specimens were collected from a depth of 40 cm. The water temperature was 16° C.

Etymology. The epithet *hyporheicus* is from the Latin, meaning "hyporheic," in reference to the habitat of this species.

Stygobromus elliotti Holsinger, 1974

Stygobromus elliotti Holsinger, 1974: 16-20, figs. 8-9 [type-locality: Deadhorse Cave, Skamania Co., Washington].

Material examined. WASHINGTON. Skamania Co.: Deadhorse Cave, 1 ♀ (TBMWSM), R. L. Crawford, 8-9 Oct. 1977; Little Red River Cave (lava tube), 1 ♀, 1 ♂ and 1 ♂ juv., R. L. Crawford and C. M. Serger, Oct. 1983.

Diagnosis. A medium-sized cavernicolous species apparently distinguished from other species of the *hubbsi* group by the long and heavily setose palpal segment 2 of maxilliped; broadly rounded outer lobes and short lateral processe of lower lip; and proportionately uneven posterior margins of the bases of pereopods 5-7. Largest ♀, 9.5 mm; largest ♂, 7.0 mm.

Distribution and ecology. This species is recorded from small streams in three lava caves in Skamania Co., Washington, two of which (Deadhorse Cave and Upper Falls Creek Cave system) are also inhabited by the stygobiont isopod *Salmasellus howarthi* (see Holsinger 1974; Lewis 2001).

Stygobromus gradyi Holsinger, 1974
(Fig. 33)

Stygobromus gradyi Holsinger, 1974: 23-26, figs. 12-

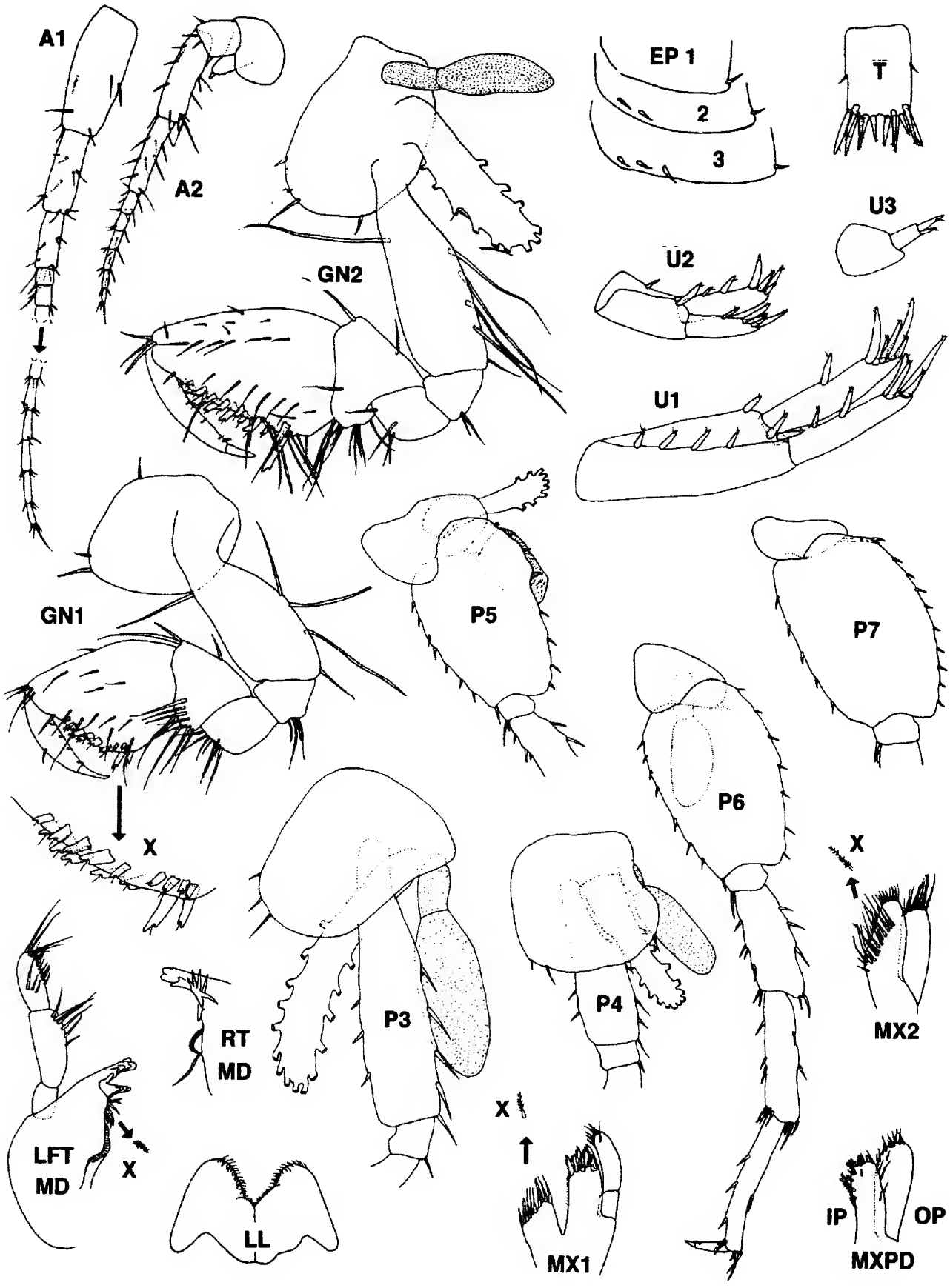

Fig. 33. *Stygobromus gradyi* Holsinger. Female (5.0 mm). Amador County, California.

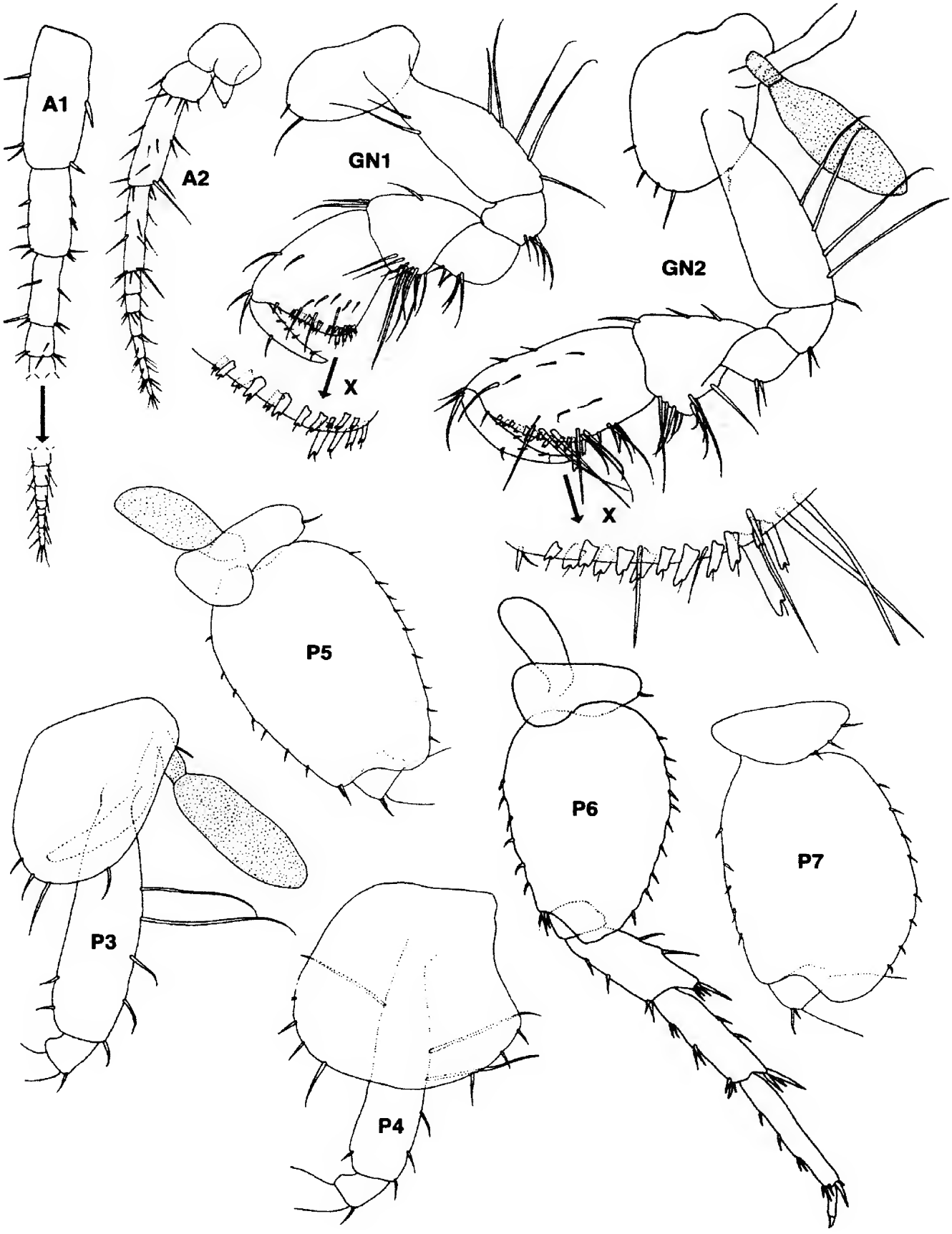

Fig. 34. ***Stygobromus latus*, n. sp.** Female (5.6 mm). Spokane County, Washington.

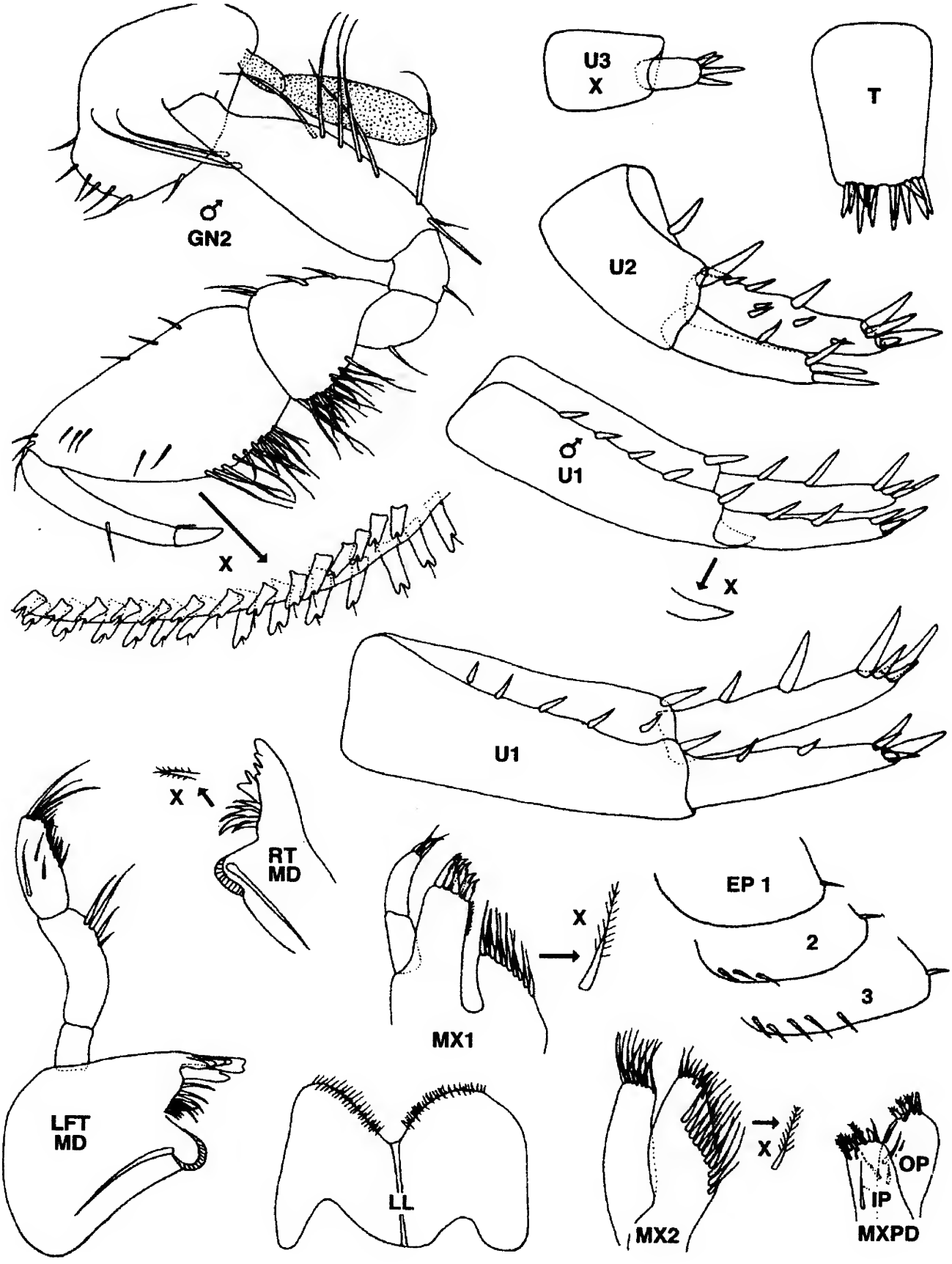

Fig. 35. ***Stygobromus latus*****, n. sp.** Female (5.6 mm); male (6.0 mm). Spokane County, Washington.

13 [type-locality: Crystal Palace Cave, Tuolumne Co., California].

Material examined. CALIFORNIA. Amador Co.: Fern Frond Cave, 7♀♀, 6♂♂, D. C. Rudolph, S. Winterath, E. van Ingen and D. Cowan, 15 Apr. 1979; unnamed spring, Masonic Cave, 1 ♀, Lulubell Cave, 1 ♀, F. G. Howarth, 17 Oct. 1987; Tuolumne Co.: small unnamed spring, ca. 14.8 km southeast of Angels Camp, 1 ♀, D. Cowan, 19 Nov. 1978.

Diagnosis. A medium-sized cavernicolous species closely related to *S. grahami* but differing from that species by smaller size at sexual maturity; lacking inner lobes on lower lip; proportionately smaller gnathopodal propod 2 of ♀, with shorter and slightly convex palm; 4 spines on ventral margins of pleonal plates 2 and 3; distally serrate peduncular process of male uropod 1. Largest ♀, 7.0 mm; largest ♂, 4.5 mm.

Distribution and ecology. This species is recorded from a small, unnamed springs and four caves in Amador and Tuolumne Cos., California.

Remarks. This species is very relatively similar morphologically to *S. grahami* and *S. harai,* and is therefore illustrated as reference point for these species (see Holsinger 1974).

Stygobromus latus, new species
(Figs. 34, 35)

Material examined. WASHINGTON. Spokane Co.: Millers Spring No. 1, about 2.6 km S. of Cheney, HOLOTYPE ♀ (USNM 1000066), 5 ♀♀ and 2 ♂♂ paratypes, I. Mohammad, 5 Dec. 1992; Millers Spring No. 2, 3 ♀♀, I. Mohammad, 5 Dec. 1992; Whitman Co.: Rock Lake Spring, 1 ♂, 3 ♀♀, I. Mohammad, 2 July 1992.

Diagnosis. A medium-sized stygobiont species, similar to *S. mysticus* in uropod 3 and broad bases of pereopods 5-7, but distinguished as follows: gnathopods 1 and 2 with more teeth on palmar margin; bases of pereopods 4-7 much broader and proportionately longer than restof segments; uropod 2 with more spines on inner ramus; telson lacking notch, proportionately deep and with more apical spines. Largest ♀, 7.5 mm; largest ♂, 6.0 mm.

Female. Antenna 1: 70 percent length of body, 50 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 5-9 plumose spines; palp segment 2 with row of 4 long setae on inner margin; palp segment 3 bearing 2 A setae, 1 B seta, 2-3 C setae, row of few D setae, and 4 E setae. Inner lobes of lower lip absent.Maxilla 1: inner plate with 10 apical, plumose setae; palp with 3 stiff setae or slender spines apically or subapically. Maxilla 2: inner plate with oblique row of 11 plumose setae on inner margin. Maxilliped: inner plate with 3 bladelike spines, 3 plumose spines, 1 naked seta apically/subapically and 1 plumose setae on inner margin; outer plate with fewer setae on inner margin and 3 lightly plumose setae on or near apex.

Gnathopod 1 propod smaller than that of gnathopod 2; palm subequal in length to posterior margin, armed with 15 spine teeth in double row; defining angle with 3 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; few inferior medial setae; dactyl nail rather short; coxa broader than deep, margin with 2 setae, one of them longer. Gnathopod 2 propod subrectangular, longer than broad; palm straight or little convex and armed with 13-14 spine teeth in double row; defining angle with 2 spine teeth of unequal length on outside, 2 shorter spine teeth on inside; posterior margin subequal to palm in length, with 2 sets of triply inserted setae; few medial setae; coxa broader than deep, margin with 5 setae.

Pereopod 3: coxal plate much deeper than broad, margin with 5 long setae. Pereopod 4: coxal plate large, broad and deep, reaching about 60-65 percent length of basis, margin with 7 setae. Pereopod 6 little longer than pereopod 7, about 46 percent length of body, 15 percent longer than pereopod 5. Pereopods 5-7: bases very broad; posterior margins convex and greatly expanded, expecially that of 7; distoposterior lobes well developed, broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively short, that of pereopod 6 about 20 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates narrow but apparently submature on material examined.

Pleonal plates: posterior margin of plate 1 nearly straight, with 1 seta near distoposterior corner, that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded; ventral margin of plate 2 with 3 spines, that of plate 3 with 5 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 66 percent length of

peduncle, with 6 spines; outer ramus with 6 spines; peduncle with 7 spines. Uropod 2: inner ramus longer than outer ramus, longer than peduncle, with 11 spines; outer ramus with 3 spines; peduncle with 2 spines. Uropod 3: peduncle usually bearing 1 or 2 small setae; ramus approximately 45-50 percent length of peduncle, with 4 apical spines.

Telson little longer than broad, gently tapered distally; apical margin with tiny median notch between spine clusters, bearing 12-13 relatively long spines.

Male. Differing from female as follows: gnathopod propods slightly shorter, palm of propod 2 shorter in relation to posterior margin and with more teeth on palmar margin. Peduncular process of uropod 1 about 25 percent length of outer ramus, pointed distally, upper margin minutely serrate; inner ramus with 6 spines; peduncle with 5 spines. Uropod 2: inner ramus with 9 spines, peduncle with 3 spines. Telson with 8 apical spines.

Distribution and ecology. This species is recorded from six springs located to the south and southwest of Cheney, WA (Mohammad 1995). They include Giffords, TNWR, Millers Springs 1 and 2, Spokane Co.; Rock Lake Spring, Whitman Co.; and Dragon Spring, Adams Co. This species co-occurs with *Stygobromus rallus* (described above) in Millers Spring No. 1 and Rock Lake Spring.

Etymology. The epithet *latus* is from the Latin, meaning "broad," in reference to the broad bases of the pereopods, which easily distinguishes this species from most others in the genus *Stygobromus*.

Remarks. This species was not described but was mentioned by Ibrahim Mohammad in his 1995 unpublished Master's thesis in the Department of Biology at Eastern Washington University, Cheney. He referred to it as "*Stygobromus* species (stocky body)."

Stygobromus gallawayae, new species
(Figs. 36, 37)

Material examined. CALIFORNIA. Butte Co.: an unnamed spring on Rock Creek, about 20.8 km N of Chico, HOLOTYPE ♀ (USNM 1000057), 2 ♂♂ paratypes, 6 juvs., J. Gallaway, 28 July 1997; 1 ♀, 1 fragment, J. Gallaway, 15 Oct 1996.

Diagnosis. A medium size stygobiont species closely related to *S. grahami* but distinguished from that species as follows: gnathopod 2 with straight or slightly concave palmar margin; pleonal plates 2 and 3 with more spines on ventral margin; uropod 1 with proportionately longer peduncle and with fewer spines; peduncle of uropod 2 with 2 spines; peduncle of uropod 3 with 1-3 spines and proportionately long and broad; telson only slightly notched. Largest ♀, 6.0 mm; largest ♂, 5.0 mm.

Female. Antenna 1: 63 percent length of body, about 70 percent longer than antenna 2; primary flagellum with 15 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 9 plumose spines; palp segment 2 with row of 6 long setae on inner margin; palp segment 3 with 8 D setae, 7 E setae, lacking A, B and C setae. Inner lobes of lower lip small. Maxilla 1: inner plate with 11 apical, plumose setae; palp with 8 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 12 plumose setae on inner margin. Maxilliped: inner plate with 3 bladelike spines, 4 plumose spines, 2 naked setae apically, and 5 plumose spines on inner margin; outer plate with setae on inner margin and 3 bladelike spines on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm about 2 times longer than posterior margin, armed with 20 spine teeth in double row; defining angle with 2 spine teeth on outside, 3 shorter ones on inside; posterior margin without setae; 2 superior medial setae; 4-6 inferior medial setae; dactyl nail short; coxa approximately 60 percent broader than deep, margin with 4 setae. Gnathopod 2: propod subrectangular, palm slightly concave medially and armed with 16 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 33 percent length of palm, with 2 sets of triply inserted setae; 8 superior medial setae, doubly inserted; 4-5 inferior medial setae, 3 long medial setae; coxa broad as deep, margin with 5 setae.

Pereopod 3: coxal plate broader than deep, margin with 4 setae. Pereopod 4: coxal plate relatively broad and deep, reaching about 50 percent length of basis, margin with 8 setae. Pereopod 6 little longer than pereopod 7, about 67 percent length of body, about 33 percent longer than pereopod 5. Pereopods 5-7: bases almost as broader proximally as distally; posterior margins slightly convex; distoposterior lobes well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with short spines; dactyls of pereopods

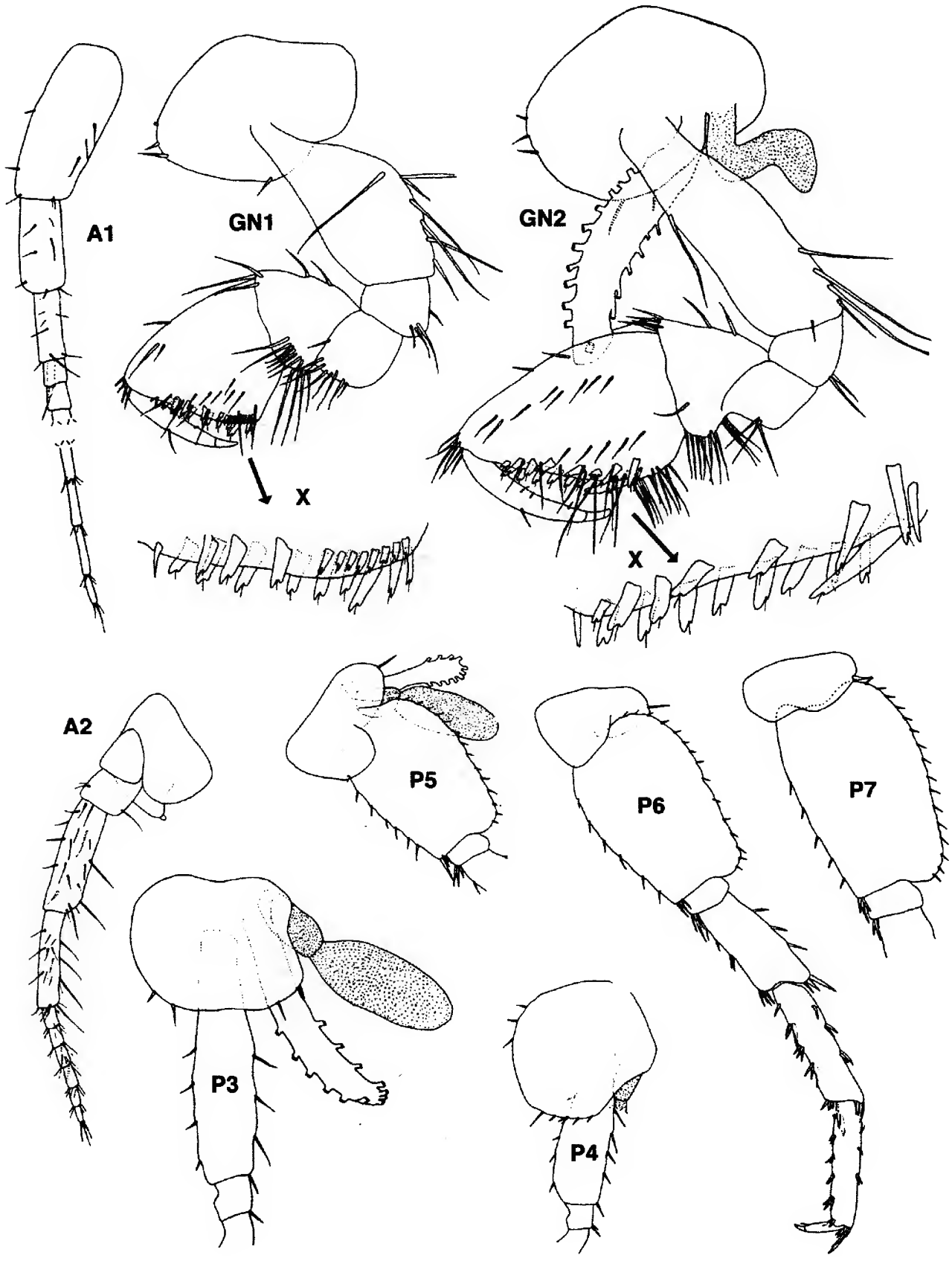

Fig. 36. ***Stygobromus gallawayae*, n. sp.** Female (6.0 mm). Butte County, California.

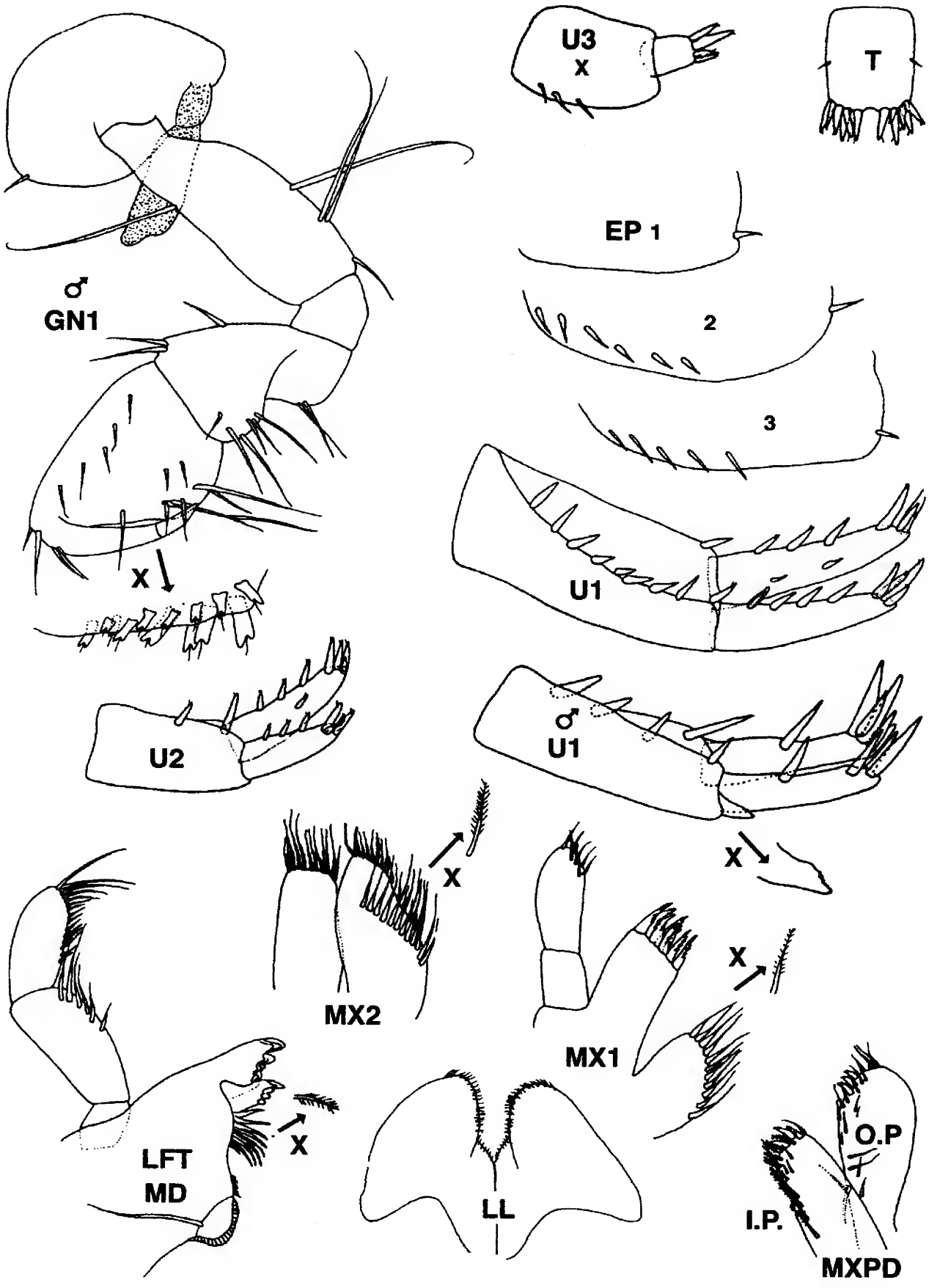

Fig. 37. ***Stygobromus gallawayae*****, n. sp.** Female (6.0 mm); male (4.8 mm). Butte Co., California.

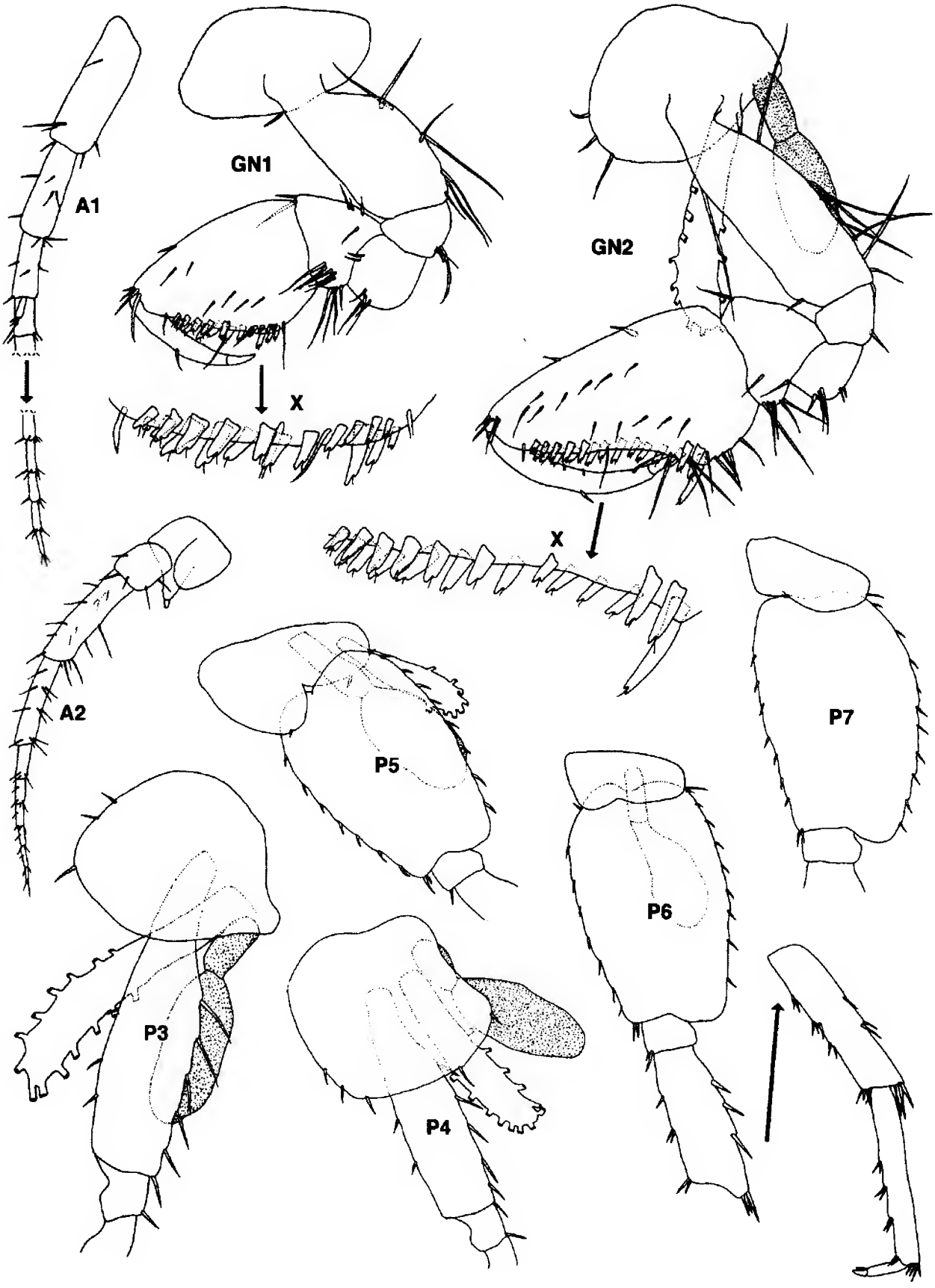

Fig. 38. *Stygobromus harai* Holsinger. Female (6.0 mm). Tuolumne County, California.

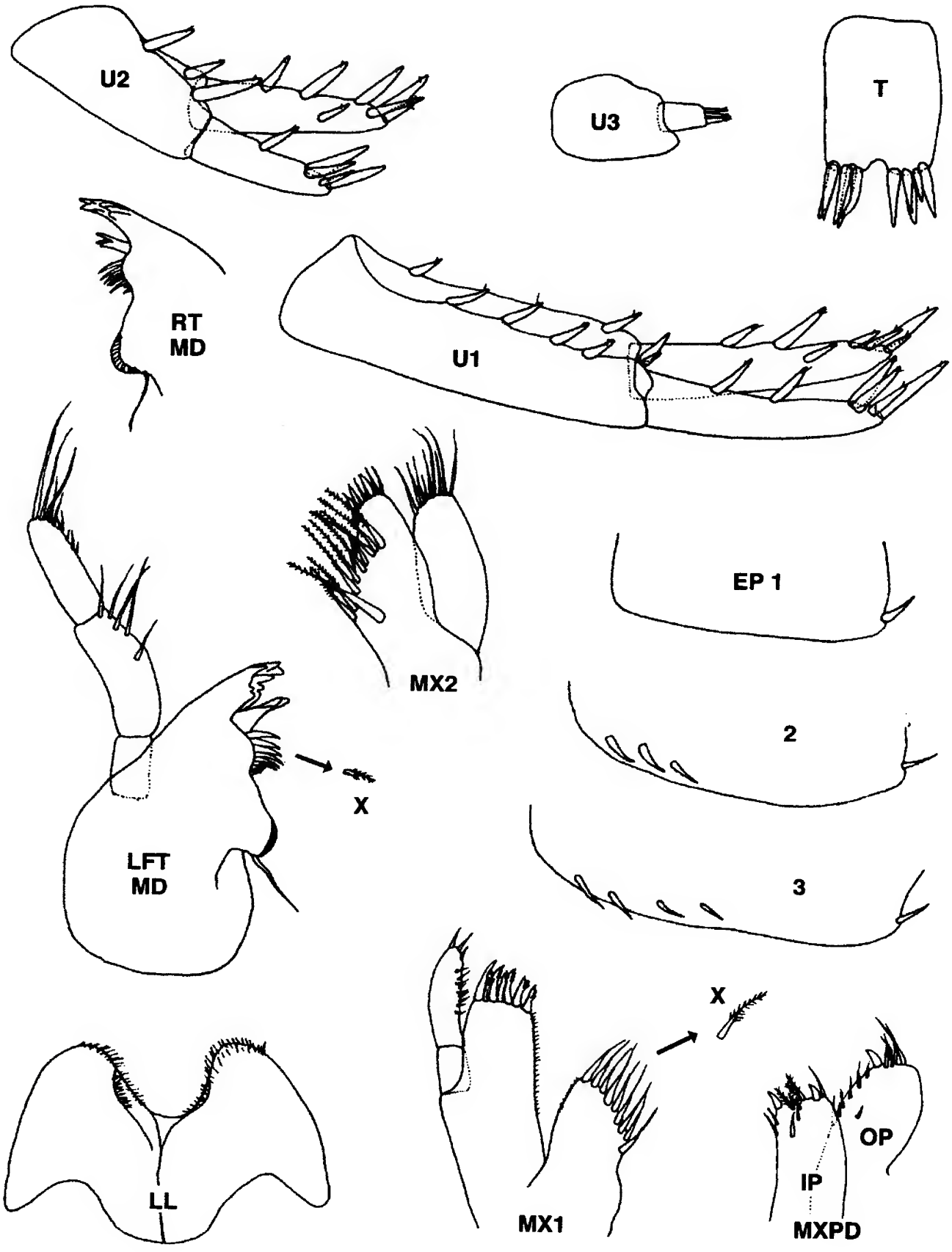

Fig. 39. *Stygobromus harai* Holsinger. Female (6.0 mm). Tuolumne County, California.

5-7 relatively slender and elongate, that of pereopod 6 about 25 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates slightly narrowing distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner, that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded; ventral margin of plate 2 with 6 spines, that of plate 3 with 5 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 75 percent length of peduncle, with 9 spines; outer ramus with 8 spines; peduncle with 10 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 8 spines; outer ramus with 7 spines; peduncle with 2 spines. Uropod 3: peduncle not bearing setae; ramus approximately 30 percent length of peduncle, with 4 apical spines.

Telson longer than broad; apical margin typically with tiny median notch between spine clusters, bearing 12 relatively long spines.

Male. Differing from female as follows: gnathopod propods smaller, palm of propod 2 longer in relation to posterior margin and with fewer teeth on margin. Uropod 1: peduncular process 33 percent length of outer ramus, narrowing sharply distally, upper margin minutely serrate; inner ramus with 5-6 spines; peduncle with 5 spines. Uropod 2: inner ramus with 6-7 spines, peduncle with 3 spines. Telson with 13-14 short apical spines.

Distribution and ecology. This species is known only from its type-locality, a spring next to Rock Creek in Butte Co., California. The temperature of the spring was about 20°C (J. Gallaway, pers. comm.).

Etymology. This species is named in honor of its collector, Ms. Jody Gallaway, who is thanked for collecting this material and allowing us to study it.

Stygobromus harai Holsinger, 1974
(Figs. 38, 39)

Stygobromus harai Holsinger, 1974: 26-29, figs. 14-15 [type-locality: Pinnacle Point Cave, Tuolumne Co., California].

Material examined. CALIFORNIA. Tuolumne Co.: Windeler Cave, near Vellecito, 1 ♀, B. Ehr, 21 Feb. 1976; 1 ♀, 2 ♂♂, W. R. Elliott, 14 Jan. 1978; unnamed spring, 15 km southeast of Sonora, 15 ♀♀, D. C. Rudolph, S. Winterath and D. Cowan, 19 Feb. 1979.

Diagnosis. A medium-sized cavernicolous species, closely similar to *S. gradyi* and *S. grahami* but differing from these 2 species as follows: fewer apical spines on inner plate of maxilliped; inner margin of posterior angle of gnathopodal propod 1 with mostly unforked spine teeth; gnathopodal propod 2 of male proportionately a little larger than propod 2 of female; coxal plates of gnathopod 2 and pereopods 3 and 4 not as deep; ramus of uropod 3 with 3 apical spines; and proportionately longer telson about one-third deeper than broad. Largest ♀, 7.5 mm; largest ♂, 7.0 mm.

Distribution and ecology. This species is recorded form two caves, one mine tunnel, and a spring, all in Tuolumne Co., California. It was collected from a pool in Windeler Cave and from beneath rocks and organic debris in the unnamed spring. The spring sample contained 1 ovigerous female (6.0 mm) with 8 embryos in the brood pouch.

Remarks. This species is closely similar morphologically to *S. grahami* and less so to *S. gradyi*, and is illustrated here as a reference point for these species.

Stygobromus wengerorum Holsinger, 1974

Stygobromus wengerorum Holsinger, 1974: 29-32, figs. 16-17 [type-locality: Bower Cave, Mariposa Co., California].

Material examined. CALIFORNIA. Mariposa Co.: Centipede Cave, 1 ♂, 6 ♀♀, S. J. Shimek, 30 July 1975.

Diagnosis. A relatively large cavernicolous species, closely similar to but differing from other cavernicolous species of the Mother Lode region by proportionately larger gnathopod propods with more spine teeth on palms and more spines on ventral margins of pleonal plates. Largest ♀, 10.0 mm; largest (and only known) ♂, 5.5 mm.

Distribution and ecology. This species is known only from two caves in Mariposa Co., California.

Taxonomic Remarks: The peduncular process present in the male is small and triangular in shape. Male otherwise like female.

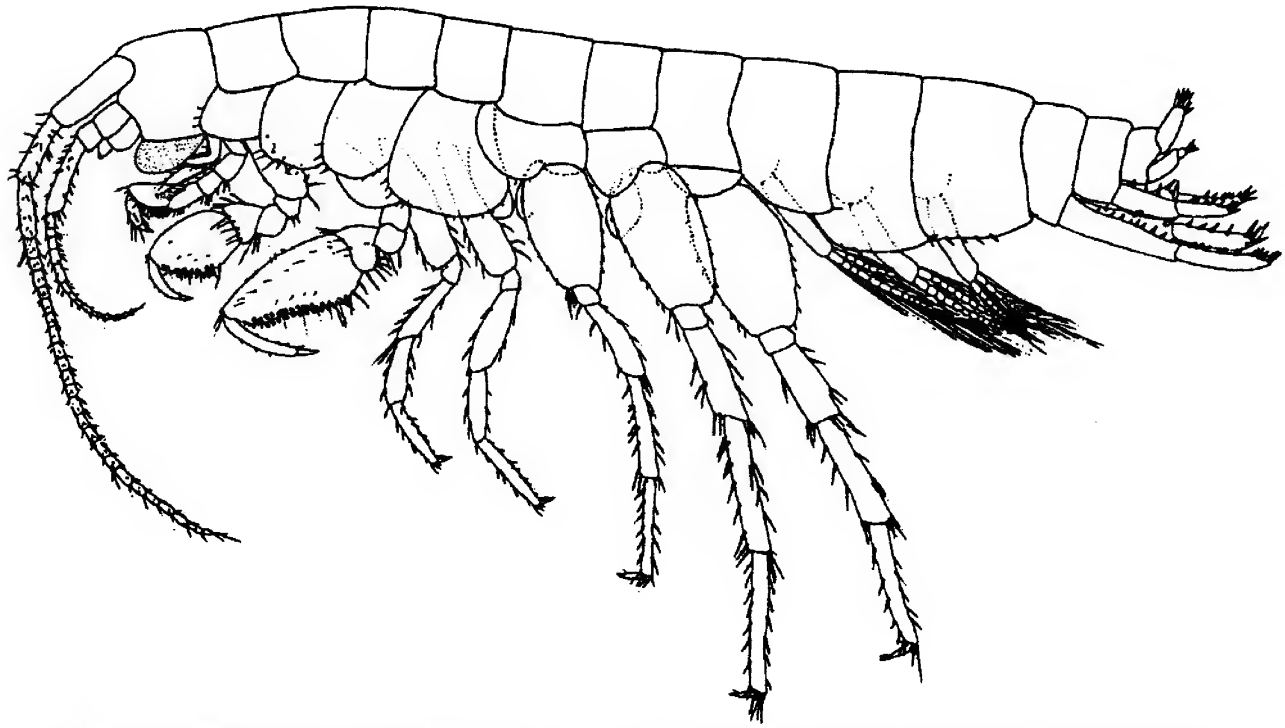

Fig. 40. *Stygobromus grahami* Holsinger. Female (9.0 mm). Calaveras County, California.

Stygobromus grahami Holsinger, 1974
(Figs. 40, 41, 42)

Stygobromus grahami Holsinger, 1974: 20-22, figs. 10-11 [type-locality: Cave of the Catacombs, Calaveras Co., California].

Material examined. CALIFORNIA. Amador Co.: Fern Frond Cave, 1 ♂, 6 ♀♀, D. C. Rudolph, S. Winterath, E. van Ingen and D. Cowan, 15 Apr. 1979; Masonic Cave, 3 ♀♀ (BBM), F. G. Howarth, 17 Oct. 1988; Calaveras Co.: Cave City Cave (= California Caverns), M. Demarest, 5 ♂♂, 22 Mar. 1996 and 31 specimens (♂, ♀ and juvs.), 2 Apr. 1996; Shaws Cave, 5 ♀♀, D. C Rudolph, S. Winterath and E. van Ingen, 17 Apr. 1979.

Diagnosis. A medium-sized cavernicolous species differing from other species of the *hubbsi* group by 15 or 16 plumose setae on apex of inner plate of maxilla 2; 12 or 13 apical spines on inner plate of maxilliped; row of forked spine teeth on the inside margin of the posterior angle of gnathopodal propod 1; deep coxal plates of gnathopod 2 and pereopod 3 and 4; more spines on ventral margins of pleonal plates 2 and 3 (except *S. hubbsi*). Largest ♀, 9.0 mm, largest ♂, 5.0 mm.

Distribution and ecology. This species is recorded from eight caves in Amador and Calaveras Cos., CA. It has been collected together with *S. gradyi* in Fern Frond (small stream) and Masonic caves in Amador County.

Remarks. This species is a rather typical member of the *hubbsi* group and is illustrated here as a reference point for comparison with other species (see also Methods and Materials).

Stygobromus rudolphi, new species
(Figs. 43, 44)

Material examined. CALIFORNIA. Santa Barbara Co.: Montgomery Spring in Los Padres National Forest, HOLOTYPE ♀ (USNM 1000070), 6 ♀♀, 1 ♂ paratypes, D. C. Rudolph, 10 May 1974.

Diagnosis. A medium-sized species closely similar to *S. grahami* and *S. gradyi* but distinguished from these 2 species as follows: palm of gnathopod 1 straight; coxal plates 1 -2 with fewer setae; coxal plates 3 and 4 broader than deep and with fewer setae; pleonal plate 2 with fewer ventral spines; peduncle of uropod 3 with a long spine; telson with more spines on apical margin. Largest ♀, 6.0 mm, largest ♂, 3.0 mm (probably immature).

Female. Antenna 1: 52 percent length of body, 57 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2: flagellum with 7 segments.

Mandibles subequal: spine row with 7-8 plumose spines; palp segment 2 with row of 6 long setae on inner margin; palp segment 3 with 3-4 C setae, 9 or more D

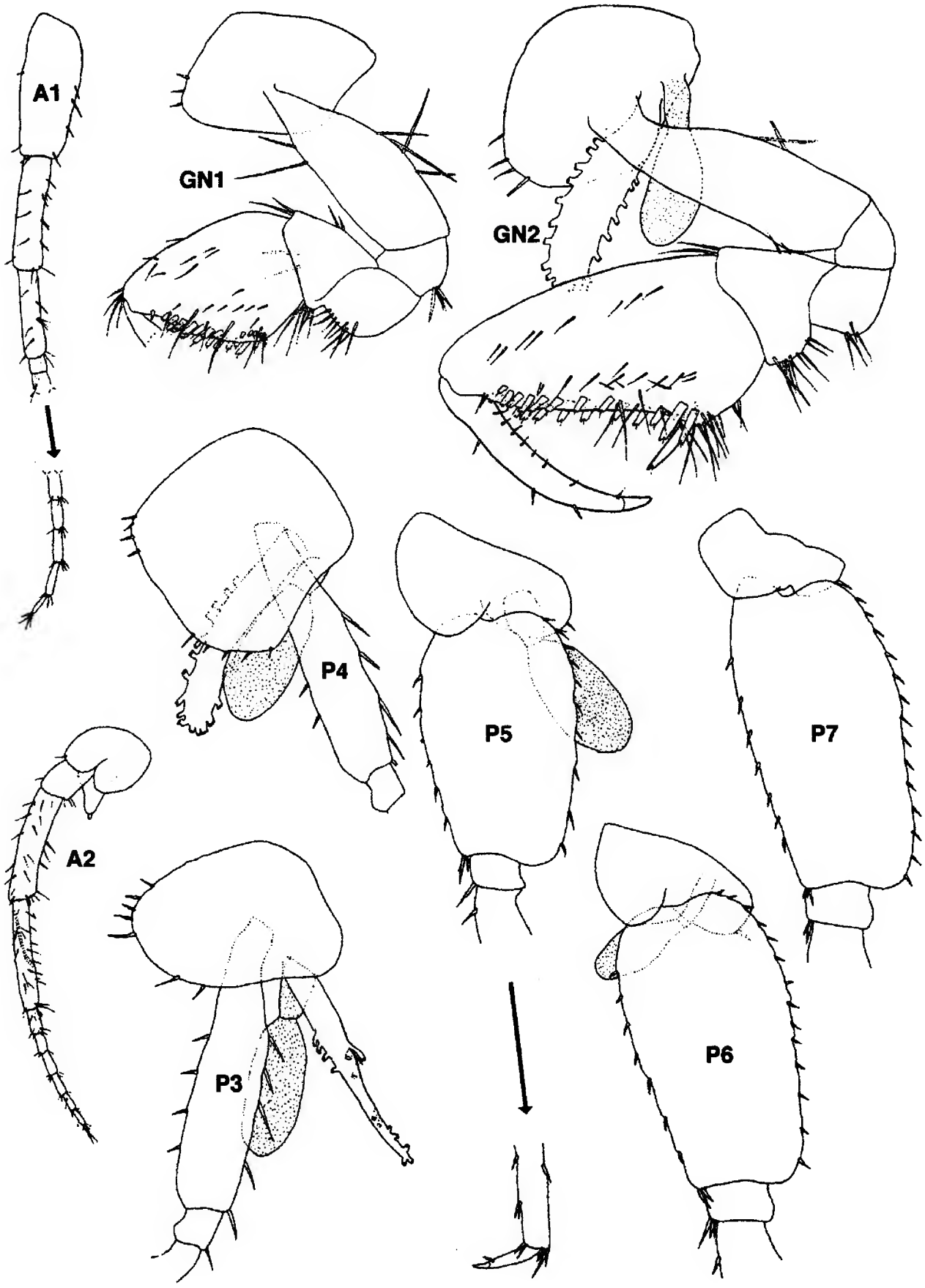

Fig. 41. *Stygobromus grahami* Holsinger. Female (6.7 mm). Amador County, California.

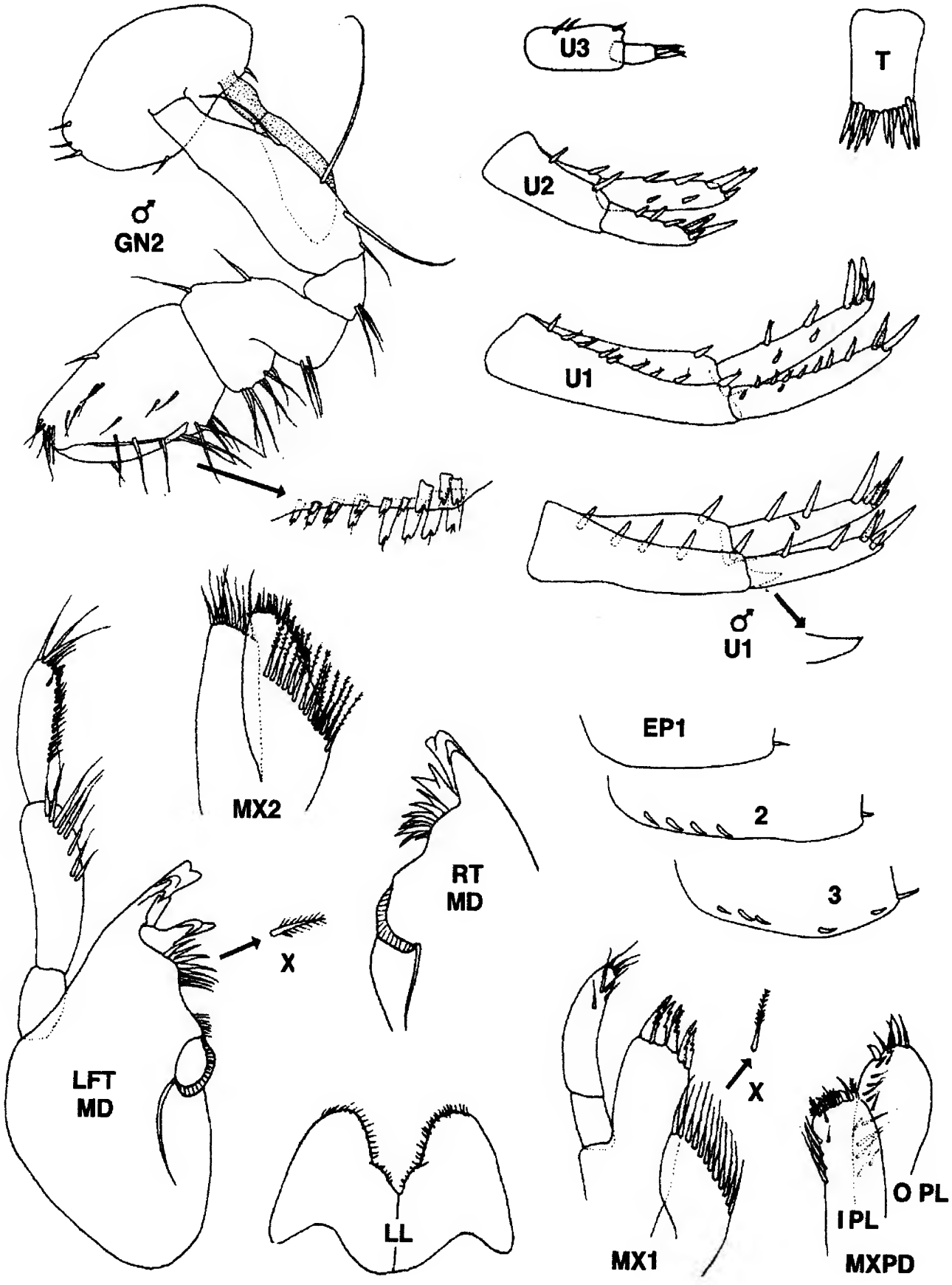

Fig.42. *Stygobromus grahami* Holsinger. Female (6.7 mm); male (5.5 mm) Amador Co., California

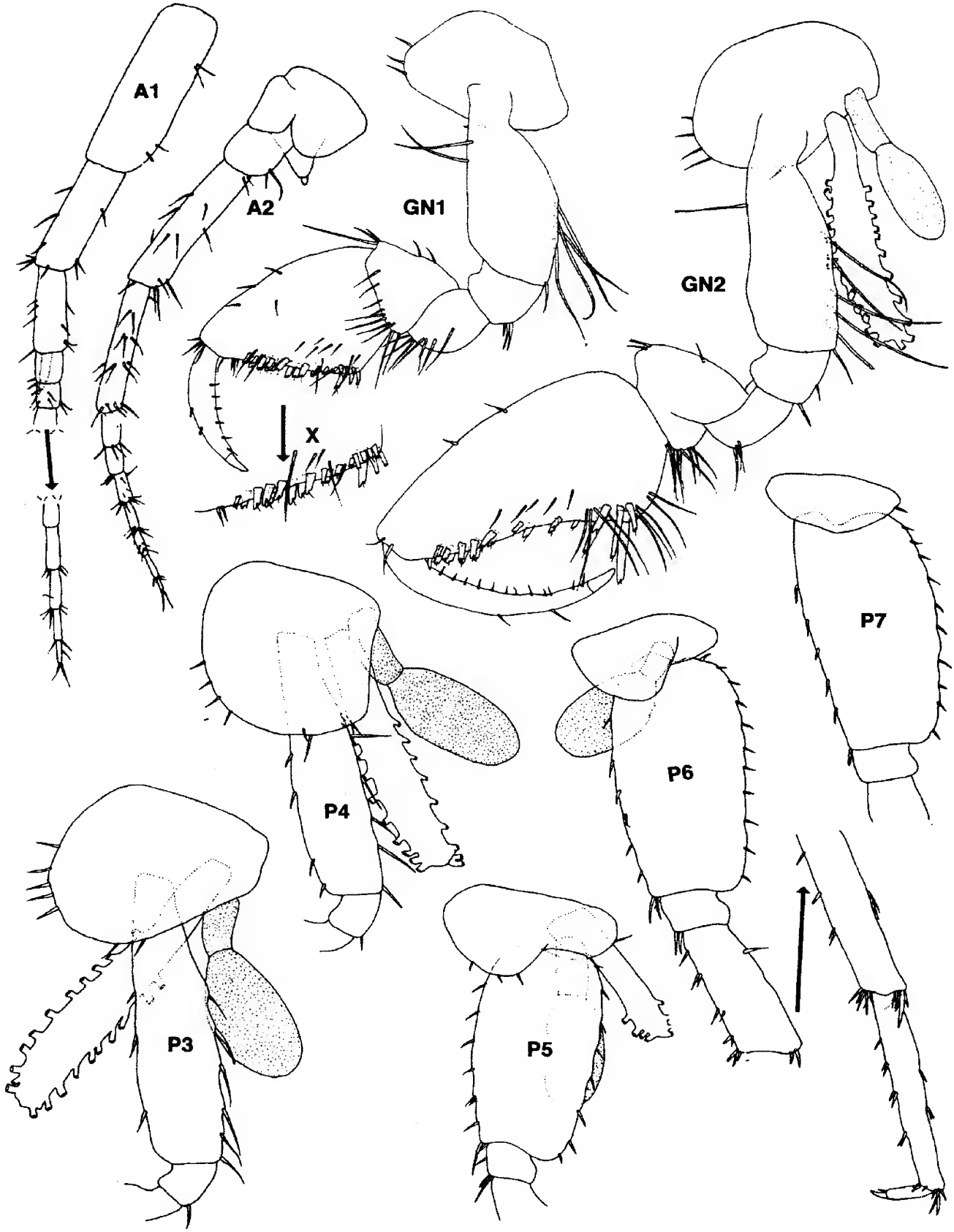

Fig. 43. ***Stygobromus rudolphi*****, n. sp.** Female (7.0 mm). Santa Barbara County, California.

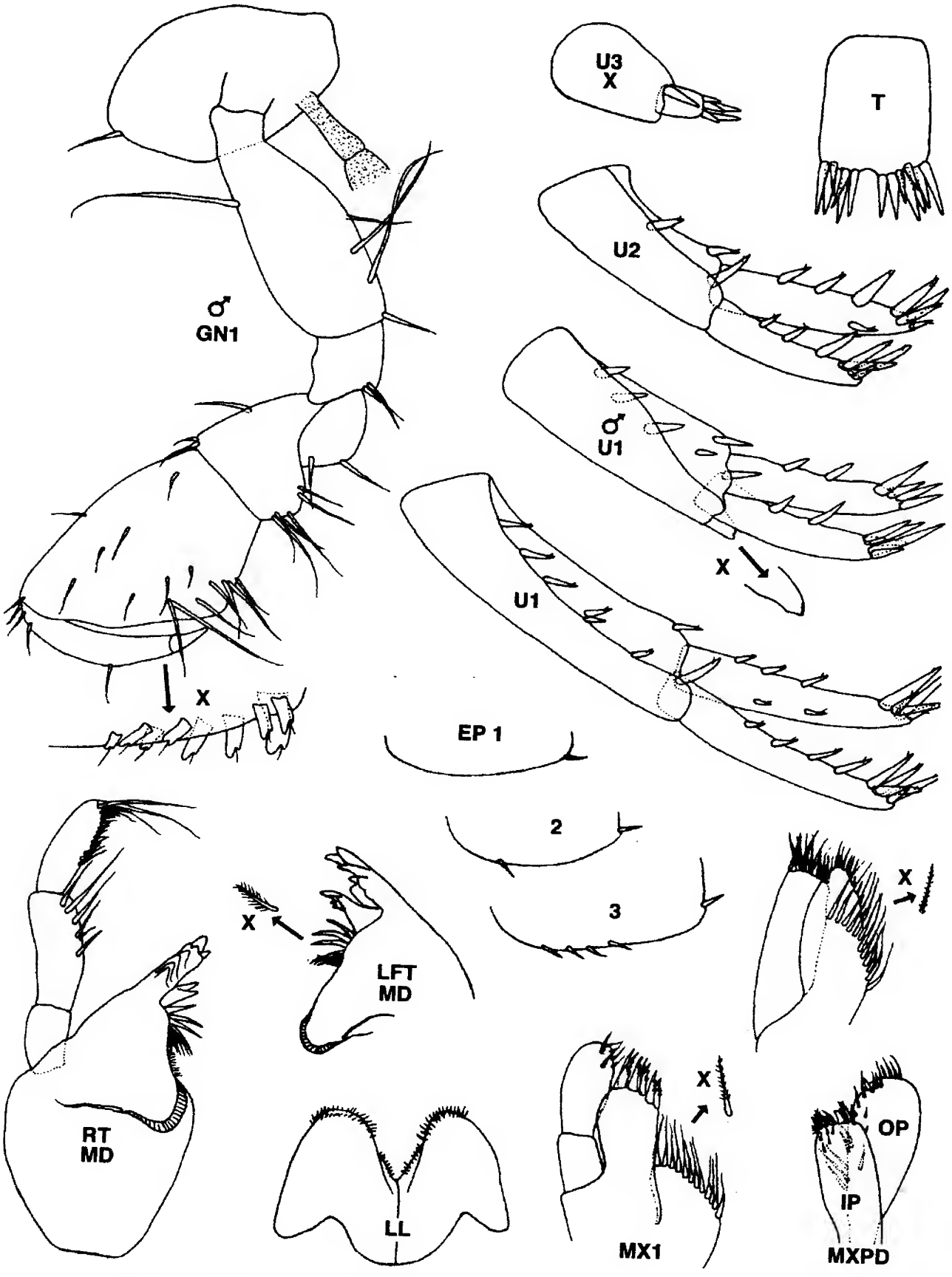

Fig. 44. ***Stygobromus rudolphi*, n. sp.** Female (7.0 mm); male (3.0 mm). Santa Barbara County, California.

setae, 4 E setae, lacking A and B setae. Inner lobes of lower lip small to vestigial.Maxilla 1: inner plate with 12 apical, plumose setae; palp with 6 stiff setae or slender spines on apical margin. Maxilla 2: inner plate with oblique row of 12 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 4 plumose spines, 3 naked setae apically, plumose spines and/or coarse setae absent from inner margin; outer plate with numerous naked setae on inner margin and lightly plumose setae on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2, palm straight, 67 percent longer than posterior margin, armed with 21 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin not bearing setae; 3-4 superior medial setae, singly inserted; 6-7 inferior medial setae; dactyl nail small; coxa broader than deep, margin with 4 setae. Gnathopod 2: propod deeper than broad; palm sinuate (concave medially) and armed with 20 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin less half length of palm, with 2 sets of doubly inserted setae; 5 medial setae; coxa broader than deep, margin with 5 setae.

Pereopod 3: coxal plate broader than deep, margin with 6 setae. Pereopod 4: coxal plate broader and deeper than that of pereopod 3, reaching about 40 percent length of basis, margin with 6 setae. Pereopod 6 little longer than pereopod 7, about 60 percent length of body, about 50 percent longer than pereopod 5. Pereopods 5-7: bases about as broad proximally as distally; posterior margins convex; distoposterior lobes well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 about 33 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from pereopod 7. Brood plates slightly expanded distally.

Pleonal plates: posterior margins of plate 1 and 3 convex, each with 1 setule near distoposterior corner, that of 2 less convex, with 1 setule near distoposterior corner; distoposterior corners rounded and distinct; ventral margin of plate 2 with 1 spine, that of plate 3 with 4 spines. Uronites free. Uropod 1: inner ramus subequal to outer ramus, about 80 percent length of peduncle, with 10 spines; outer ramus with 9 spines; peduncle with 8 spines. Uropod 2: inner ramus longer than outer ramus, little longer than peduncle and with 8 spines; outer ramus with 7 spines; peduncle with 3 spines. Uropod 3: peduncle bearing one spine apically; ramus approximately 33 percent length of peduncle, bearing 5 apical spines.

Telson longer than broad, apex with tiny median notch between spine clusters, bearing 14 relatively long spines.

Male. Differing from female as follows: palm of gnathopod 2 shorter in relation to posterior margin; palmar margin convex and with fewer teeth; Uropod 1: peduncular process 25 percent length of outer ramus, inner ramus with 6 spines; peduncle with 6 spines. Uropod 2: inner ramus with 7-8 spines, peduncle with 3-4 spines. Telson with 14-17 long apical spines.

Distribution and ecology. This species is known only from its type-locality, Montgomery Spring,which is apparently developed in sandstone. Specimens were collected from a water tank fed by a small seep-like spring in the San Rafael Mountains (D. C. Rudolph, pers. comm.).

Etymology. This species is named in honor of its collector, D. Craig Rudolph, who discovered it during a survey of the subterranean invertebrates of California.

Stygobromus imperialis, new species
(Figs. 45, 46)

Material examined. CALIFORNIA. Santa Cruz Co.: Empire Cave, HOLOTYPE ♀ (on slide mounts in part) (USNM 1000062), D. C. Rudolph, D. Cowan and B. van Ingen, 22 Apr. 1979.

Diagnosis. A relatively large cavernicolous species closely similar to *S. grahami* but distinguished as follows: palp segment 2 of mandible with 6 rather long setae on inner margin; maxillae 1 and 2 with more setae on inner plates; posterior margin of propod of gnathopod 2 with 1 -3 setae; coxal plate of pereopods 3 and 4 deeper and with more setae; more spines on ventral margins of pleonal plates 2 and 3; uropod 3 with fewer apical spines. Largest ♀, 9.2 mm, ♂ unknown.

Female. Antenna 1: about 58 percent length of body, 70 percent longer than antenna 2; primary flagellum with 18 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal, spine row with 8-9 plumose spines; palp segment 2 with 6 rather long setae on inner

margin; palp segment 3 with 4-5 C, 13 D and 4 E setae, lacking both A and B setae. Inner lobes of lower lip small to vestigial. Maxilla 1: inner plate with 13 apical plumose setae; palp with 9 stiff setae apically or subapically. Maxilla 2: inner plate with oblique row of 14 plumose setae on inner margin. Maxilliped: inner plate with 3 bladelike spines, 2 plumose spines, and 3 naked setae apically/subapically, 3 plumose spines on inner margin; outer plate with setae on inner margin; 7 setae and 1 bladelike spine on or near apex.

Gnathopod: propod smaller than that of gnathopod 2; palm 2 times longer than posterior margin, armed with 30 spine teeth in double row; defining angle with 4 spine teeth on outside, 6 shorter ones on inside; posterior margin without setae; 8 superior medial setae, 5 inferior medial setae; dactyl nail rather shorter; coxa about 33 percent deeper than broad, margin with 3 setae. Gnathopod 2: propod subrectangular, longer than broad; palm sinuate, armed with 25 - 26 spine teeth in double row; defining angle with 2 spine teeth of unequal length on outside, 3 long spine teeth on inside; posterior margin about 1/3 length of palm, with few setae; 8 superior medial setae, 9 inferior medial setae; dactyl nail shorter; coxa broader than deep, margin with 5 setae.

Pereopod 3: coxal plate deeper than broad, margin with 9 setae. Pereopod 4: coxal plate relatively broad and deep, subquadrate, reaching about 45 percent length of basis, margin with 9 setae. Pereopod 6 little longer than pereopod 7, about 65 percent length of body, 20 percent longer than pereopod 5. Pereopods 5-7: bases broader proximally than distally; posterior margins convex (but not greatly expanded); distoposterior lobes moderately well developed, broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively shorter, that of pereopod 6 typically 25 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from pereopod 7. Brood plates somewhat narrowing distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 seta near distoposterior corner, that of 2 and 3 less convex, each with 1 seta near distoposterior corner; distoposterior corners rounded; ventral margin of plate 2 with 3 spines, that of plate 3 with 5 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 60 percent length of peduncle, with 7 spines; outer ramus with 9 spines; peduncle with 10 spines. Uropod 2, inner ramus longer than outer ramus, subequal in length to peduncle, with 9 spines; outer ramus with 5 spines; peduncle with 4 spines. Uropod 3, peduncle not bearing setae; ramus approximately 30 percent length of peduncle, with 2 apical spines.

Telson little longer than broad, gently tapered distally, apical margin with tiny median notch between spine clusters, bearing about 10 relatively long spines.

Distribution and ecology. The species is known only from a single female specimen. This species was collected from a cave pool up to 1 m in depth (D. C. Ruldolph, pers. comm.). It was taken together with 5 specimens of *Stygobromus mackenziei*.

Etymology. The epithet *imperialis* is from the Latin, meaning "imperial," in reference to the type-locality, Empire Cave.

Other Species

The following nine species from western North America have not been assigned to the *hubbsi* group and are treated separately in this section. They are distinguished from species of the *hubbsi* group by possessing sternal gills (or processes).

Stygobromus canadensis Holsinger, 1980

Stygobromus canadensis Holsinger, 1980: 290-297, figs. 1 [type-locality: Castleguard Cave, Alberta, Canada]; Holsinger, 1981: 93 - 95; Holsinger et al. 1983: 546 - 547.

Diagnosis. A small to medium-sized subterranean species, distinguished from all other species of *Stygobromus* by presence of paired sternal gills on pereonites 2-5, also distinguished by having few segments of pleopod rami, and having simple, paired lateral sternal gills on pereopods 6 and 7. Largest ♀, 5.0 mm; largest ♂, 5.5 mm.

Distribution and ecology. To date this species is known only from a stream in its type-locality, Castleguard Cave. This is a large alpine-type cave situated partly beneath a glacier and located about 90 km south of Cadomin in Banff National Park, Alberta, Canada (see Holsinger 1980; Holsinger et al. 1983).

Stygobromus idahoensis, new species
(Figs. 47, 48)

Material examined. IDAHO. Lemhi Co.: Shallow hyporheic habitat at mouth of Wilson Creek, a tributary to the middle

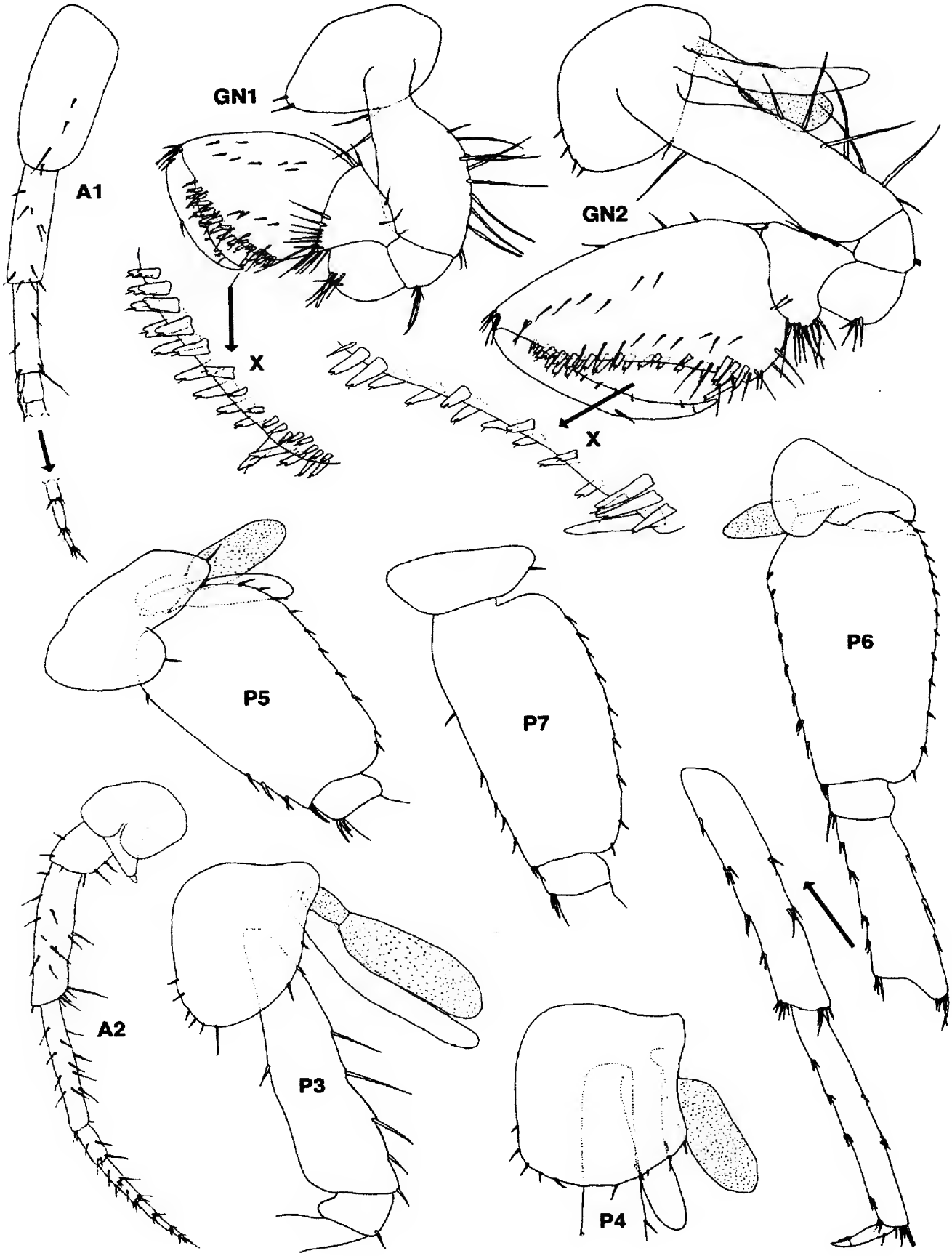

Fig. 45. ***Stygobromus imperialis*, n. sp.** Female (9.2 mm). Santa Cruz County, California.

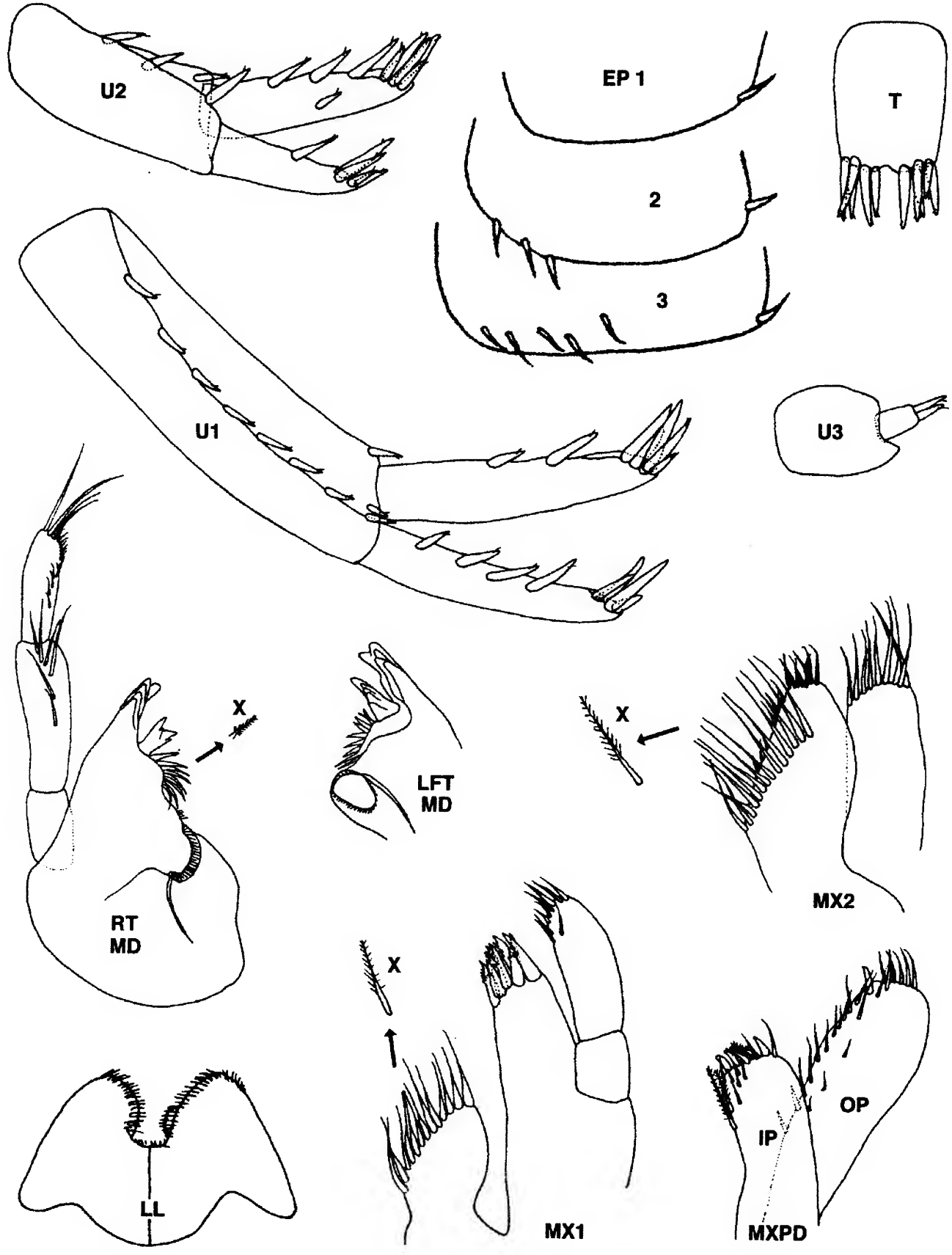

Fig. 46. ***Stygobromus imperialis*, n. sp.** Female (9.2 mm). Santa Cruz County, California.

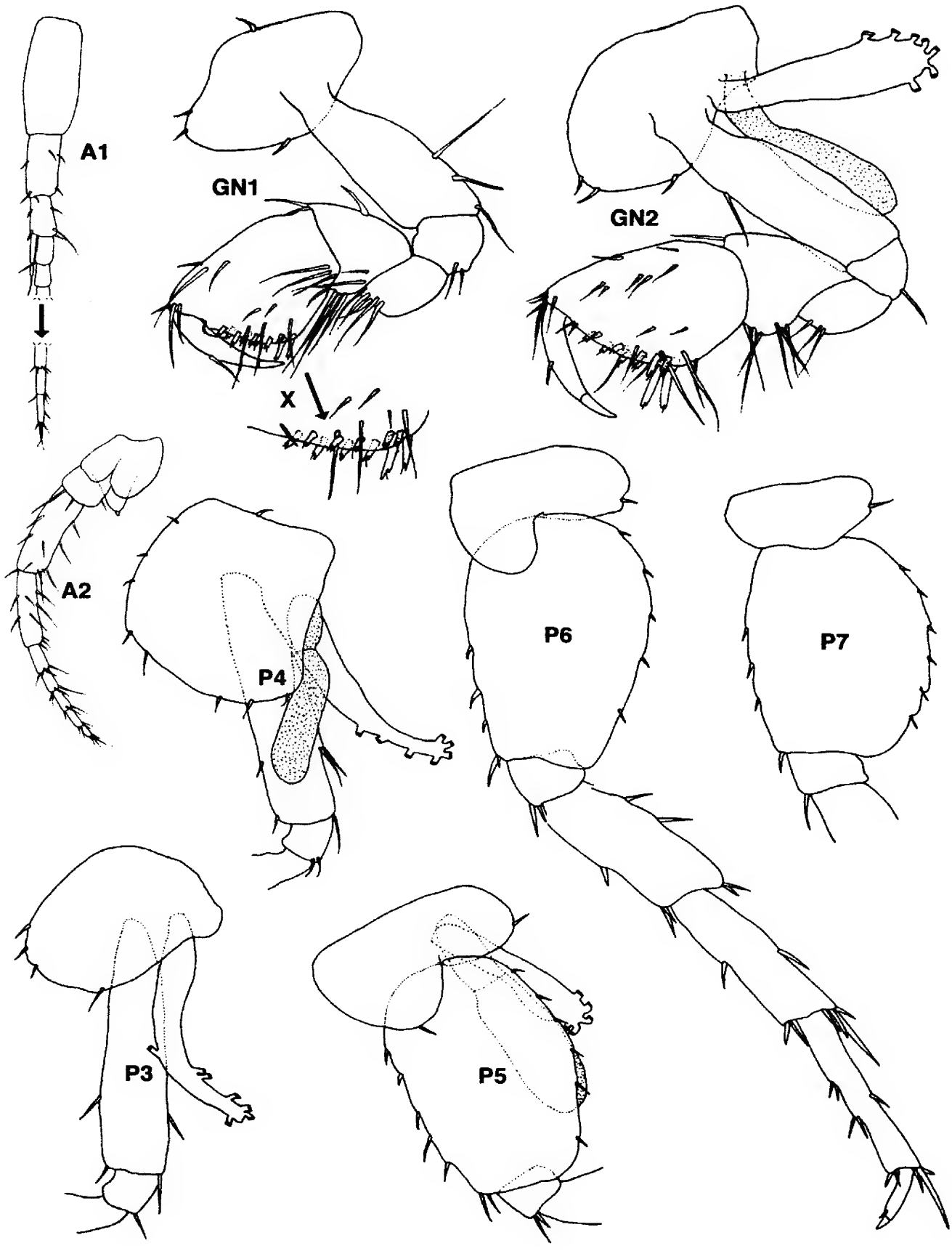

Fig. 47. ***Stygobromus idahoensis*, n. sp.** Female (3.5 mm). Lemhi County, Idaho.

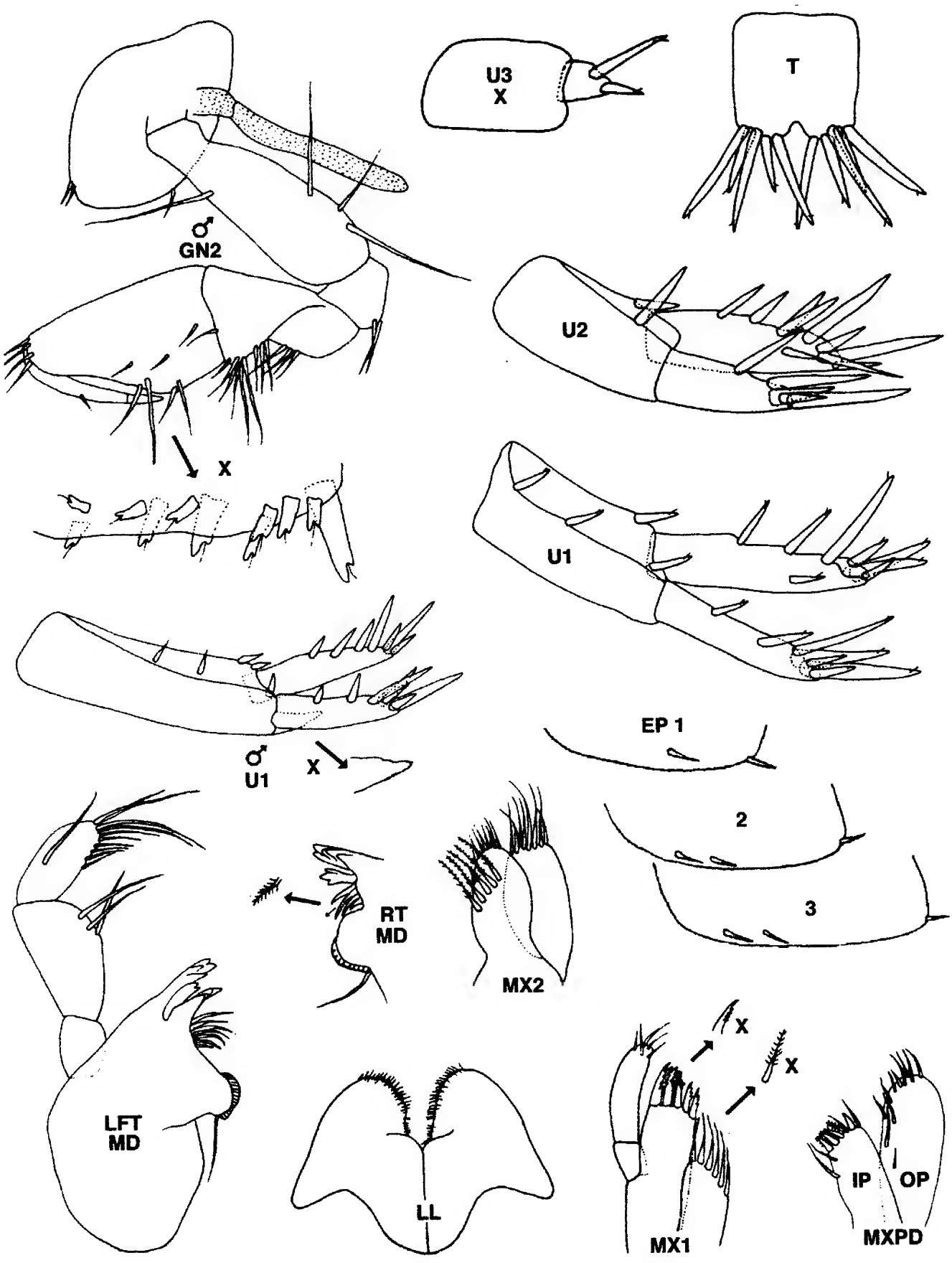

Fig. 48. ***Stygobromus idahoensis*, n. sp.** Female (3.5 mm); male (3.0 mm). Lemhi County, Idaho.

fork of Salmon River [45° 02'57" N, 114° 43'31" W.), coll. - HOLOTYPE ♀ (USNM 1000061), 1 ♂ and 3 ♀♀ paratypes, P. Koetsier, probably late 1986 (no exact date on the collection label).

Diagnosis: A small groundwater species, distinguished by small size, rather broad bases of pereopods 5 - 7, especially 7; 2 long spine teeth at defining angle of propod of gnathopod 2; and apically heavily spinose uropods 1 and 2. Largest ♀, 3.5 mm, largest ♂, 3.0 mm.

Female. Antenna 1: 47 percent length of body, 40 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 5-7 plumose spines; palp segment 2 with row of 3 rather long setae on inner margin; palp segment 3 bearing 1 B seta, 6 D setae, and 4 E setae, lacking both A and C setae. Inner lobes of lower lip small to vestigial. Maxilla 1, inner plate with 6 apical, plumose setae; palp with 5 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 5 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 4 plumose spines, and 2-3 naked setae apically, and 2 plumose setae on inner margin; outer plate with setae on inner margin and 6-7 lightly plumose setae on or near apex.

Gnathopod 1: propod little smaller than propod of gnathopod 2; palm straight, little longer than posterior margin, armed with 11 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; 3 superior medial setae; 2 -3 inferior medial setae; dactyl nail moderately short; coxa approximately about as broad as deep; margin with 4 setae. Gnathopod 2, propod longer than broad; palm straight or weakly convex and armed with 11 spine teeth in double row; defining angle with 2 long spine teeth on outside, 2 shorter spine teeth on inside; posterior margin shorter than palm, with 1 or 2 setae; few superior medial setae doubly and singly inserted; 2 singly inserted inferior medial setae; dactyl nail moderately long; coxa deeper than broad; margin with 3 setae.

Pereopod 3, coxal plate deeper than broad, margin with 4 setae. Pereopod 4, coxal plate relatively broad and deep, reaching about 55 percent length of basis, margin with 9 setae. Pereopod 6 little longer than pereopod 7, about 54 percent length of body, 20 percent longer than pereopod 5. Pereopods 5-7, bases broadest proximally; posterior margins of 5 and 7 strongly convex and expanded, that of 6 less so; distoposterior lobes distinct and broadly rounded; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 about 35 - 40 percent length of corresponding propod. Coxal gills present on pereopods 2 - 6, absent from 7. Simple, lateral sternal gills present on pereonites 6 and 7. Brood plates slightly narrowing distally.

Pleonal plates: posterior margins of plates 1 - 3 weakly convex, with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 1 with 1 spine, that of plates 2 and 3 with 2 spines each. Uronites free. Uropod 1: inner ramus little longer than outer ramus, 10 percent longer than length of peduncle, with 8 spines, 1 elongate; outer ramus with 7 spines, 3 elongate; peduncle with 4 spines. Uropod 2: rami heavily spinose apically; inner ramus longer than outer ramus, subequal in length to peduncle, with 11 spines; outer ramus with 5-6 robust spines; peduncle with 2 spines. Uropod 3: peduncle without setae, ramus only 30 percent length of peduncle, with 2 apical spines.

Telson subquadrate, about as long as broad, apical margin with tiny median notch between spine clusters, bearing 10 relatively long spines, some as long as telson.

Male. Differing from female as follows: gnathopod propods narrower, palm of propod 2 shorter in relation to posterior margin and with fewer teeth on palmar margin. Uropod 1: peduncular process about 50 percent length of outer ramus, tapering to blunt point distally, upper margin minutely serrate toward apex; inner ramus with 7-8 spines; peduncle with 5 spines. Uropod 2: inner ramus with 9-12 spines, peduncle with 3 spines. Telson, with 13-14 long apical spines.

Distribution and ecology. This species is known only from its type-locality, where according to Peter Koetsier (pers. comm.), the material was collected with a Surber bottom sampler.

Etymology. This species is named for the state of Idaho.

Stygobromus glacialis, new species
(Fig. 49)

Material examined. MONTANA. Glacier Co.: Zoo Cave, about 16 km W of Babb Glacier Nat. Park, HOLOTYPE ♀ (USNM 1000058), 1 ♀ paratype, J. Chester, 27 Aug. 1977; Flathead Co.: Algal Cave, 2 ♀♀, J. Chester, 25 Aug. 1977;

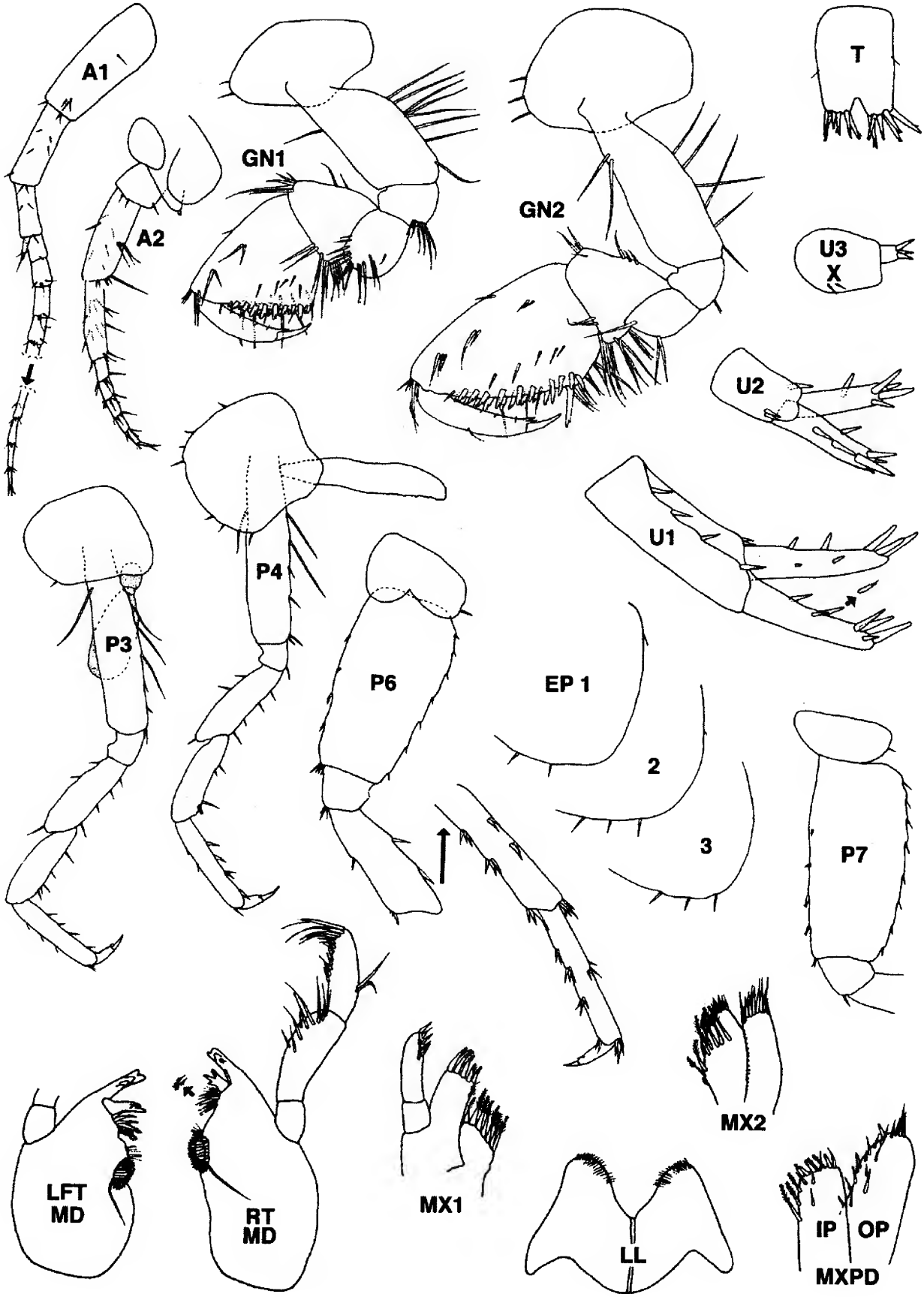

Fig. 49. ***Stygobromus glacialis*, n. sp.** Female (6.5 mm). Glacier County, Montana.

4 ♀♀, P. Hendricks, 27 Sept. 1999; Logan Creek springhead, Logan Pass, 100(+) specimens, (♀, ♂ juv.) (MTEC), J. Giersch, 20 Aug. 2000; stream in an unnamed cave on Trail Creek in Flathead National Forest, ca. 12.8 km S of Canadian border, 1 ♀, J. A. Stanford, 25 Nov. 1980.

Diagnosis. A relatively small to medium-sized cavernicolous species, distinguished from all other species of *Stygobromus* by the possession of 3 pairs of lateral sternal gills on pereonites 5, 6 and 7; and further distinguished by slender bases of pereopods 5-7, and several setules each on posterior margins of pleonal plates. Largest ♀, 7.0 mm; largest ♂, 4.5 mm.

Female. Antenna 1: 40 percent length of body, 40 percent longer than antenna 2; primary flagellum with 13 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 7-8 plumose spines; palp segment 2 with row of 9 long setae on inner margin; palp segment 3 bearing 2 B setae, 9 D setae, and 4 setae E, lacking both A and C setae. Inner lobes of lower lip vestigial or absent. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 8 stiff setae apically. Maxilla 2: inner plate with oblique row of 7 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 5 plumose spines, 2 naked setae apically, and 3 plumose spines on inner margin; outer plate with setae on inner margin and 3 lightly plumose setae on or near apex.

Gnathopod 1: propod smaller than that of gnathopod 2; palm straight and almost 2 times longer than posterior margin, armed with 18 spine teeth in double row; defining angle with 2 spine teeth on outside, 1 shorter one on inside; posterior margin lacking setae; 4 doubly inserted superior medial setae; 5 inferior medial setae; dactyl nail long and slender; coxa approximately 2 times broader than deep, margin with 2 setae. Gnathopod 2: propod longer and broader than first pereopod, longer than broad; palm straight or little convex medially, armed with 20 spine teeth in double row; defining angle with 1 spine tooth on outside, 3 shorter spine teeth on inside; posterior margin 33 percent length of palm, with 2 sets of doubly inserted setae; 7 - 8 superior medial setae doubly and triply inserted, about 5 singly inserted inferior medial setae; coxa broader than deep, margin with 3 setae.

Pereopod 3: coxal plate deeper than broad, margin with 1 setae. Pereopod 4: coxal plate relatively broad and about as broad as deep, reaching about 45 percent length of basis, margin with 7 setae. Pereopod 6 little longer than pereopod 7, about 50 percent length of body, 25 percent longer than pereopod 5. Pereopods 5-7: bases little broader proximally than distally; posterior margins slightly convex; distoposterior lobes poorly developed and indistinct; anterior and posterior margins with 2-4 spines and setae; segments 4, 5 and 6 of pereopods 5-7 with slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 approximately 30 percent length of corresponding propod. Coxal gills on pereopods 2 - 6, absent from 7. Three pairs of long, slender simple lateral sternal gills present on pereonites 5 - 7, longest on 6 and 7. Brood plates rather narrow, not setose on specimen illustrated.

Pleonal plates: posterior margins of plates 1 - 3 convex, each with 2 or 3 setules; distoposterior corners rounded and indistinct; ventral margins of plates 1-3 lacking spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 7 spines; outer ramus with 7 spines; peduncle with 6 spines. Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 5 spines; outer ramus with 7 spines; peduncle with 3 spines. Uropod 3: peduncle usually bearing 1-2 small setae; ramus approximately 20 percent length of peduncle, with 3 apical spines.

Telson longer than width, apical margin with small median notch, bearing 12 relatively long spines.

Distribution and ecology. The species is recorded from Zoo Cave in Glacier County and Algal Cave (= West Tunnel Cave), an unnamed cave on Trail Creek and Logan Creek springhead in adjoinning Flathead County. Algal and Zoo caves and the spring are in Glacier National Park, whereas the unnamed cave is just outside the park's western boundary. According to Paul Hendricks (pers. comm.), who made the most recent collection of this species from Algal Cave in 1999, the specimens were taken from a series of three silt-bottom pools with a slight flow between them. He also reported seeing 30-40 amphipods that were not collected. Stygobiont isopods, *Salmasellus stegonathrix* Bowman also inhabit the pools (Lewis 2001). The 2 ovigerous females measured 5.8 mm long and each had 2 embryos in the brood pouch, although 4 embryos were lost in the vial. The other females were 5.0 mm long and had setose brood plates but were not ovigerous. The temperature of the Algal Cave stream pools was 6.5°C.

A very recent (August 2000) collection of this species was made by Joe Giersch, who obtained a large sample of more than 100 individuals form the Springhead of Logan Creek in Logan Pass at an elevation of 2159 m. According to J. Giersch (pers. comm.)

the species is abundant in gravels in the substrate of the spring flow.

Etymology. The epithet *glacialis* is from the Latin, meaning "ice" or "frozen" in reference to the occurrence of this species in Glacier National Park.

Stygobromus secundus Bousfield & Holsinger, 1981

Stygobromus secundus Bousfield and Holsinger, 1981: 1827-1830, figs. 1 [type-locality: a spring 24 km southwest of Rocky Mountain House, Alberta, Canada].

Diagnosis. A small to medium-sized groundwater species, distinguished from all other species of Stygobromus by presence of simple, median sternal gills on pereonites 2 and 3 and simple, paired, lateral sternal gills on pereonites 4, 5, 6 and 7; and also distinguished by comparatively large ramus of uropod 3 (but less than half length of peduncle); and absence of a peduncular process on uropod 1 of the male. Largest ♀, 5.2 mm; largest ♂, 4.0 mm.

Distribution and ecology. This species is known only from its type-locality (see Bousfield and Holsinger 1981).

Stygobromus obscurus Holsinger, 1974

Stygobromus obscurus Holsinger, 1974: 55-58, figs. 34-35 [type-locality: well at Victor Crossing, Ravalli Co., Montana].

Diagnosis. A small to medium-sized subterranean species, apparently unrelated to other known species of *Stygobromus* in western North America and distinguished by: relatively slender propods of gnathopods; shallow coxal plates of gnathopod 2 and pereopods 3 and 4; narrow bases of pereopods 5-7 which lack distoposterior lobes; 2 pairs of simple, lateral sternal gills on pereonites 6 and 7; absence of ventral spines on pleonal plates; heavily spinose uropods and telson; and relatively long spines on uropods 3 and telson. Largest ♀, 7.0 mm; ♂ unknown.

Distribution and ecology. This species is known only from its type-locality, collected along with two other species of *Stygobromus* (see Holsinger 1974).

Stygobromus montanensis Holsinger, 1974

Stygobromus montanensis Holsinger, 1974: 52-55, figs. 32-33 [type-locality: well at Victor Crossing, Ravalli Co., Montana].

Diagnosis. A small to medium-sized subterranean species, distinguished by possession of few setae on posterior margin of gnathopod propod 1 and presence of 2 pairs of tiny, simple lateral sternal gills on pereonites 6 and 7; 4 relatively long spines on ramus of uropod 3 (Holsinger 1974). Largest ♀, 5.5 mm; ♂ unknown.

Distribution and ecology. This species is known only from its type-locality, where it has been collected with two other species of *Stygobromus* (see Holsinger 1974).

Stygobromus curroae, new species
(Figs. 50, 51)

Material examined. NEW MEXICO. Taos Co.: groundwater discharge into Gallina Creek, Sangro de Cristo Mountains. near Taos, HOLOTYPE ♀ (USNM 1000054), 2 ♀♀ paratypes, J. Curro, 23 Nov. 1994 and 1 ♂, 5 July 1994.

Diagnosis. A relatively small goundwater species, with some resemblance to *S. holsingeri* and *S. arizonensis* but easily distinguished as follows: maxillae 1 and 2 with fewer setae on inner plates; palm of propod of gnathopod 1 with more spine teeth; coxal plates 3 and 4 with more setae; relative long distally expanded telson, with 18 - 20 apical spines and rather deep notch; uropods 1-2 with more long and thick spines on rami; and tiny, simple, lateral sternal gills on pereonites 6 and 7. Largest ♀, 4.8 mm; largest ♂, 4.5 mm.

Female. Antenna 1: 55 percent length of body, 40 percent longer than antenna 2; primary flagellum with 12 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 6 plumose spines; palp segment 2 with row of 6 setae on inner margin; palp segment 2 with 6 long setae in inner margin; palp segment 3 bearing 1 B seta, 5 C setae, 9 D setae, and 3 E setae, lacking A setae. Inner lobes of lower lip absent. Maxilla 1: inner plate with 6 apical, plumose setae; palp with 6 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 3 bladelike spines, 2 plumose spines, 1 naked seta apically, and 1 plumose spine on inner margin; outer plate with setae on inner margin, and 1 lightly plumose seta and 1 bladelike spine on or near apex.

Gnathopod 1: propod little smaller than that of gnathopod 2; palm straight or slightly convex, approximately 2 times longer than posterior margin, armed

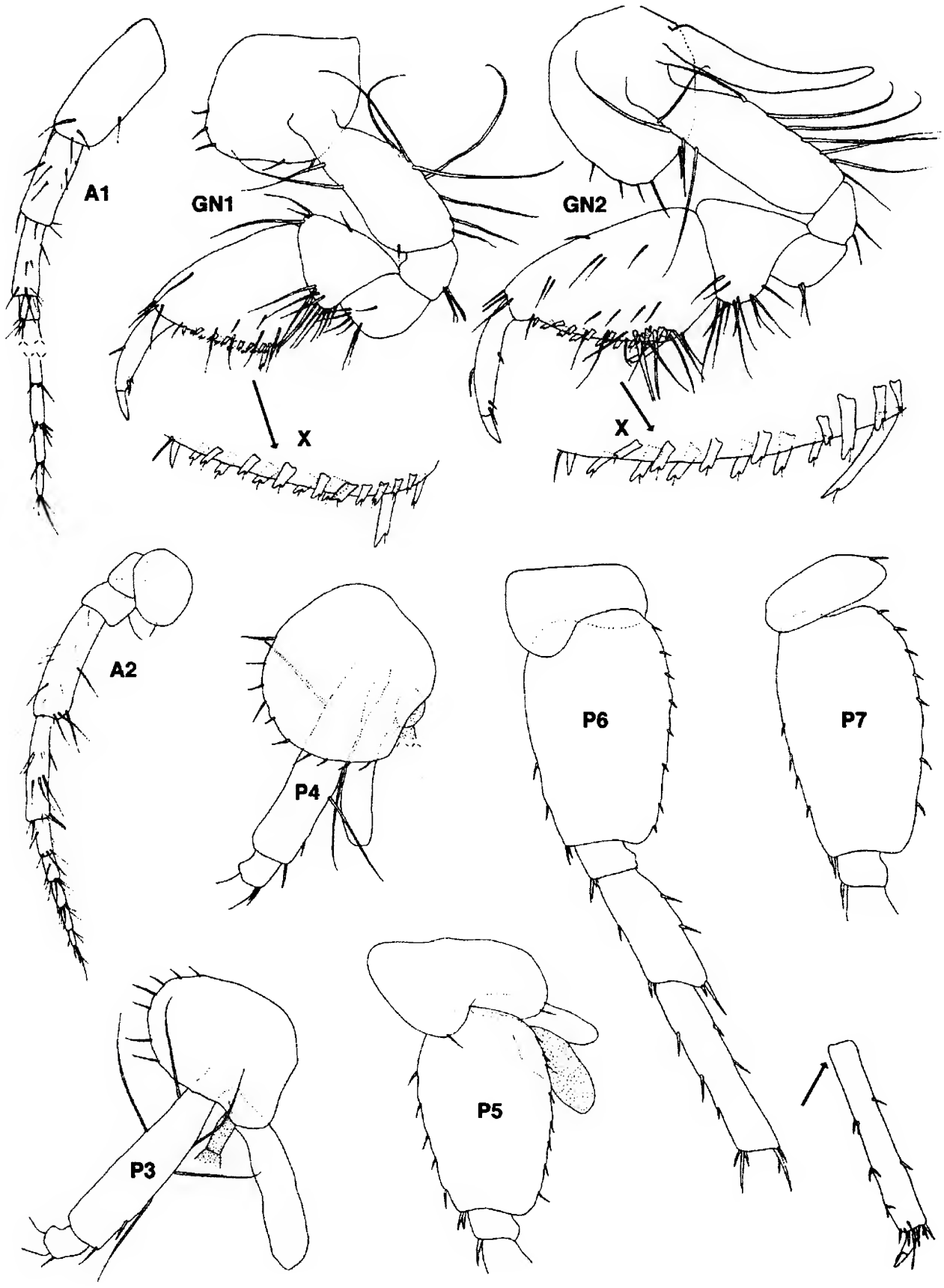

Fig. 50. ***Stygobromus curroae*, n. sp.** Female (4.4 mm). Taos County, New Mexico.

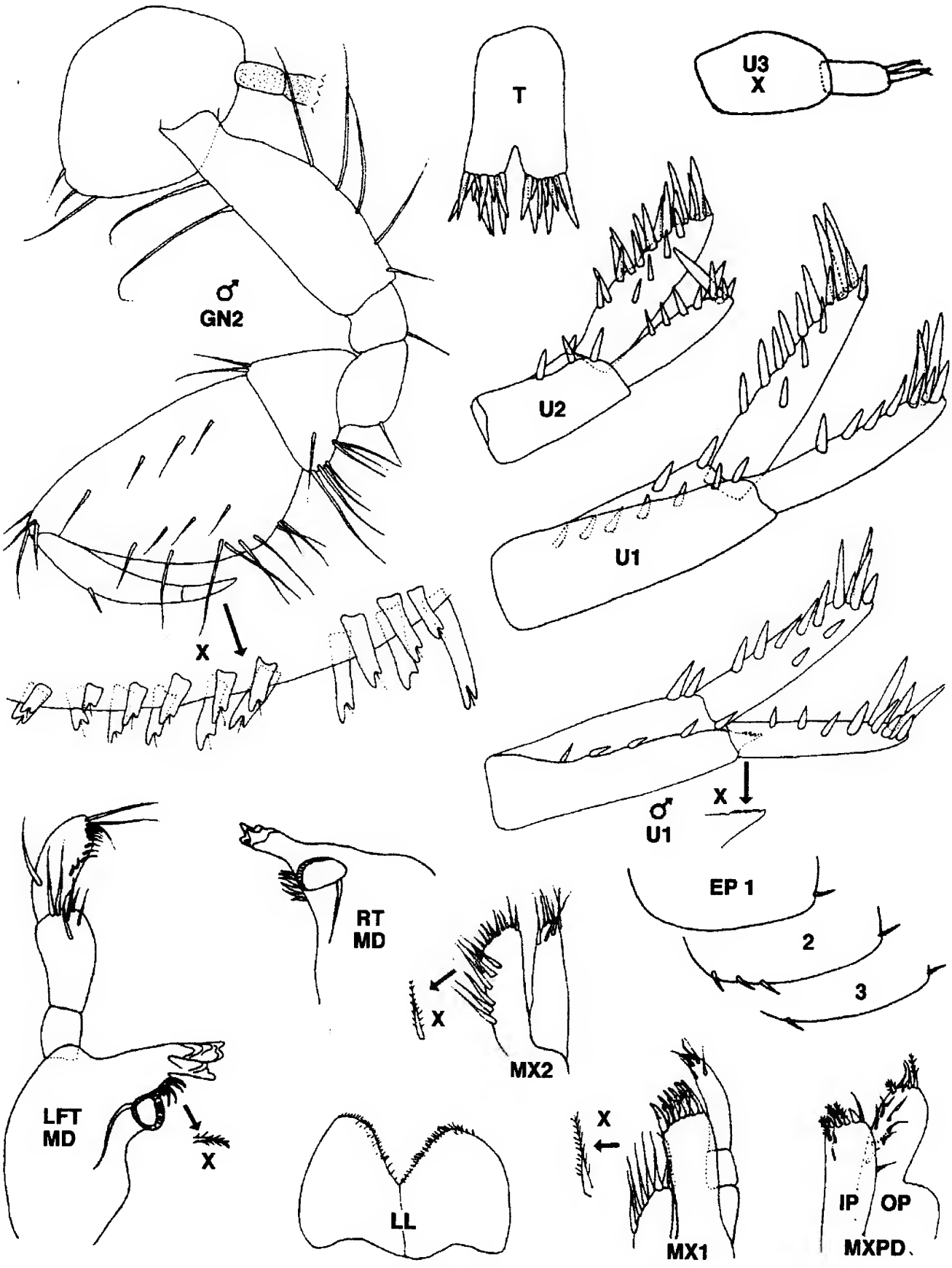

Fig. 51. ***Stygobromus curroae*, n. sp.** Female (4.4 mm); male (4.5 mm). Taos Co., New Mexico.

with 16 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter ones on inside; posterior margin without setae; 1 superior medial setae; 2-3 inferior medial setae; dactyl nail relatively short; coxa little broader than deep, margin with 5 setae. Gnathopod 2: propod deeper than broad; palm straight or slightly convex and armed with 15-16 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 1 or 2 setae; 4 - 5 doubly inserted superior medial setae; 4 inferior medial setae; coxa little broader than deep, margin with 5 setae.

Pereopod 3: coxal plate deeper than broad, margin with 7 setae. Pereopod 4: coxal plate relatively broad and deep, reaching about 50 percent length of basis, broadly convex margin with 10 setae. Pereopod 6 little longer than pereopod 7, about 77 percent length of body, 42 percent longer than pereopod 5. Pereopods 5-7: bases broader proximally than distally; posterior margins convex; distoposterior lobes well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively slender and short, that of pereopod 6 approximately 25 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from pereopod 7. Two pairs of tiny, simple lateral sternal gills on pereonites 6 and 7.Brood plates little expanded distally, but not setose in material examined.

Pleonal plates: posterior margin of plates 1 - 3 convex, each with 1 setule near distoposterior corner; distoposterior corners rounded, indistinct; ventral margin of plate 2 with 3 spines, that of plate 3 with 1 spine. Uronites free. Uropod 1: inner ramus spinose, little longer than outer ramus, about 95 percent length of peduncle, with 15 mostly robust spines; outer ramus with 10 spines; peduncle with 9 spines. Uropod 2: inner ramus longer than outer ramus, heavily spinose, longer than peduncle, with approximately 20 spines; outer ramus with 9 spines, 1 very large; peduncle with 4 spines. Uropod 3: peduncle usually bearing 1 or 2 small setae; ramus approximately 55 percent length of peduncle, with 2 apical spines.

Telson 25 - 30 percent longer than broad, gently expanded distally; apical margin typically with relatively deep V-shaped median notch between spine clusters, bearing 19-20 relatively long spines.

Male. Differing from female as follows: gnathopod propods slightly broader, palm of propod 2 shorter in comparison with posterior margin, with more teeth on palmar margin. Uropod 1: peduncular process sharply pointed distally, with lightly serrate upper margin, approximately 20 percent length of outer ramus; inner ramus with 14-15 spines; peduncle with 7 spines. Uropod 2: inner ramus with approximately 22-25 spines, peduncle with 4-5 spines. Telson with 18-21 apical spines.

Distribution and ecology. This species is known only from its type locality, where it was sampled from the hyporheic zone with a PVC pipe and pump from a depth of 30 cm (J. Curro, pers. comm.).

Etymology. This species is named in honor of its collector, Julia Curro.

Stygobromus simplex, new species
(Fig. 52)

Material examined. COLORADO. Rio Blanco Co.: Spring Cave, southeast of Meeker, HOLOTYPE ♀ (on slide mounts in part) (USNM 1000071), M. Tate and K. Tate, 4 Oct., 1995.

Diagnosis. A medium-sized cavernicolous species that resembles *S. holsingeri* in structure of gnathopods and uropods 2-3, but is distinguished from that species as follows: maxilla 1-2 with fewer setae on inner plate; maxilliped with bladelike spines on inner plate; gnathopods 1-2 with more teeth on palmar margin; bases of pereopods 3-7 with fewer spines on posterior margins; pleonal plates 2 - 3 with more ventral margin spines; and presence of relatively long, lateral sternal gills. Largest ♀, 5.0 mm, ♂, unknown.

Female. Antenna 1: 44 percent length of body, 34 percent longer than antenna 2; primary flagellum with 10 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 4-6 plumose spines; palp segment 2 with row of 6 rather long setae on inner margin; palp segment 3 with 8 D setae, 4 E setae, without A, B and C setae. Inner lobes of lower lip vestigial or absent. Maxilla 1: inner plate with 6 apical, plumose setae; palp with 6 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 2 bladelike spines, 3 plumose spines, 2 naked setae apically, and 2 plumose setae on inner margin; outer plate with setae on inner margin and apex.

Gnathopod 1: propod little shorter than that of gnathopod 2; palm weakly convex, about 2 times longer than posterior margin, armed with 21-22 spine teeth in double row; defining angle with 2 spine teeth on

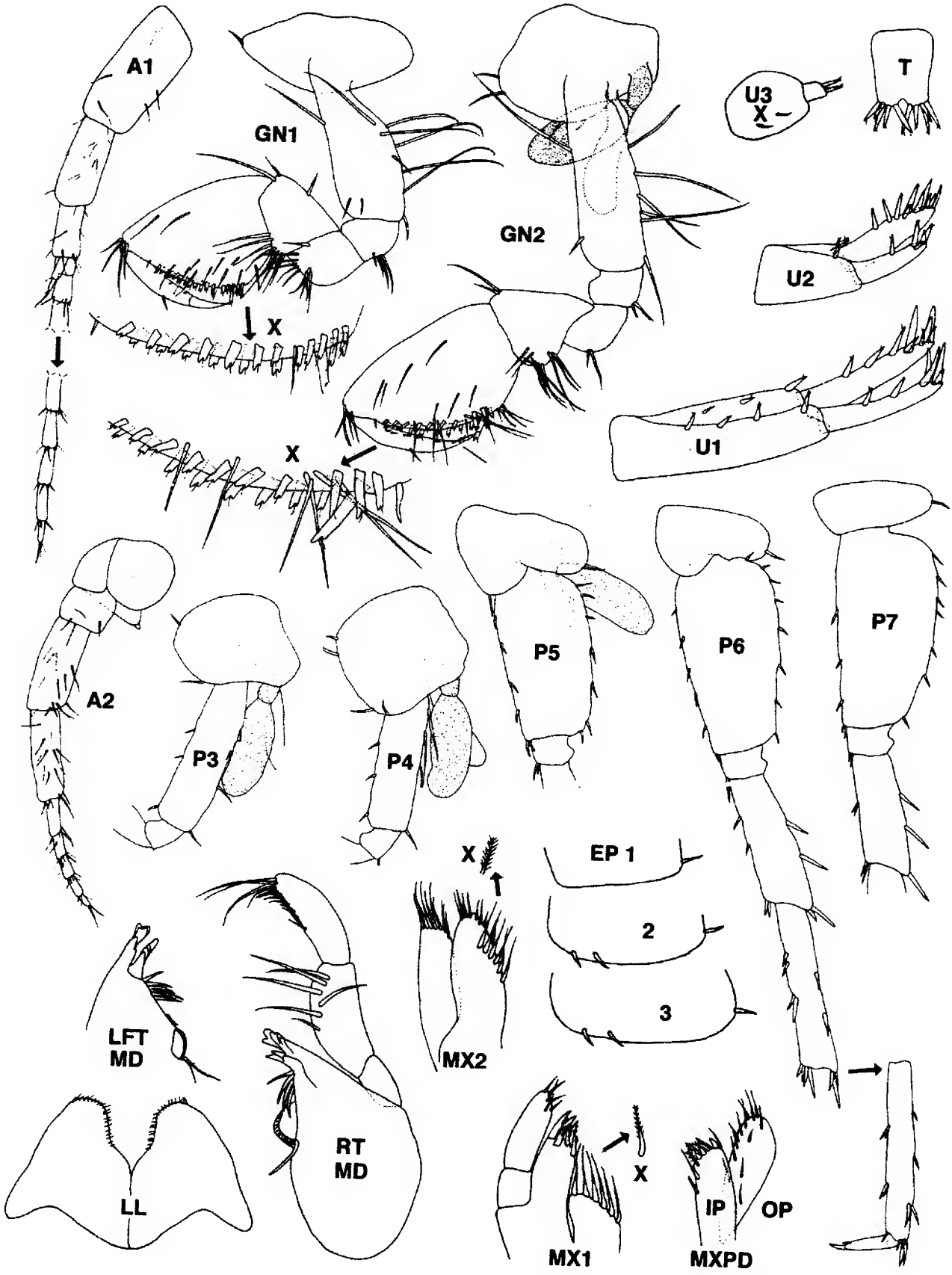

Fig. 52. ***Stygobromus simplex*, n. sp.** Female (5.0 mm). Rio Blanco County, Colorado.

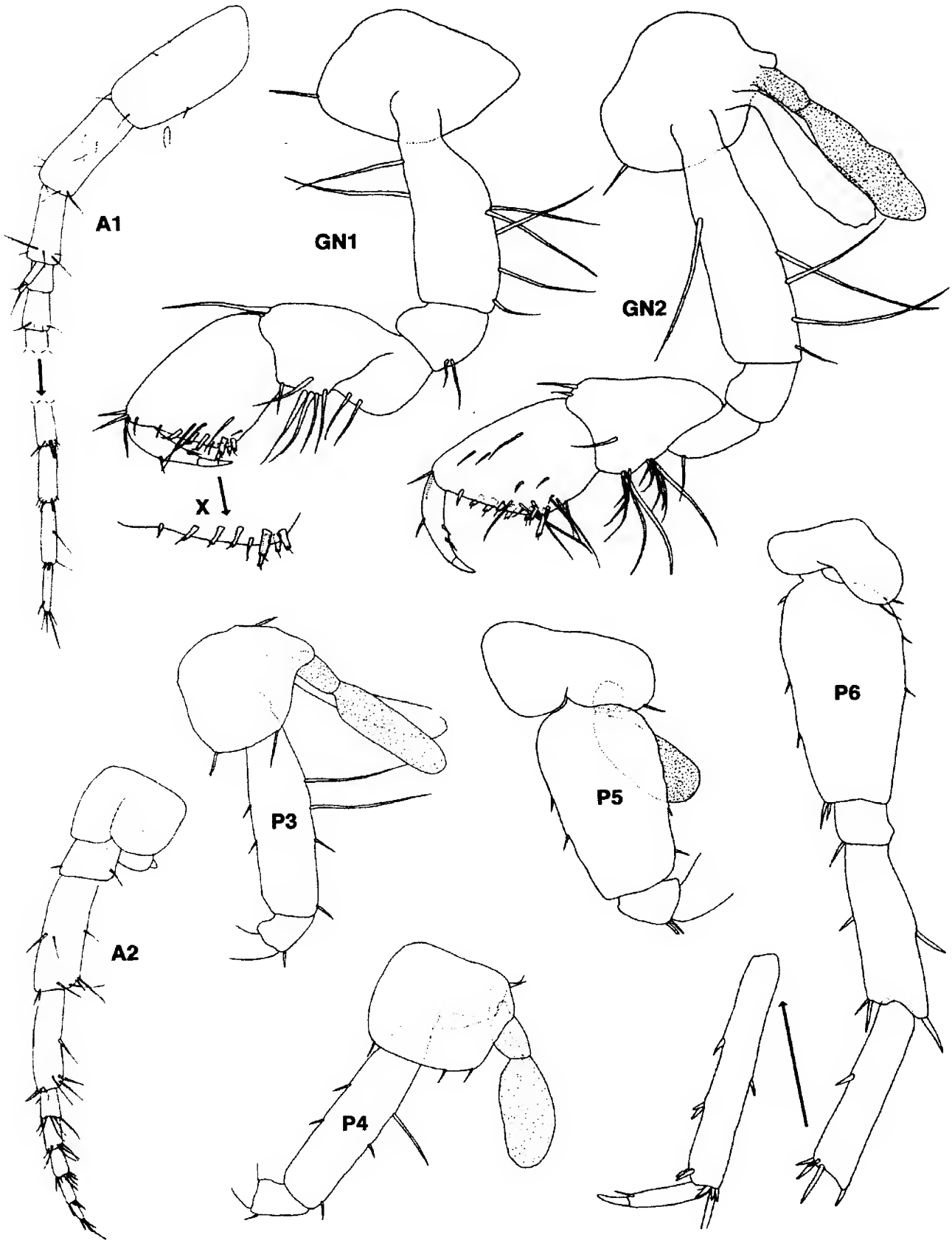

Fig. 53. *Stygobromus wardi*, n. sp. Female (3.7 mm). Eagle County, Colorado.

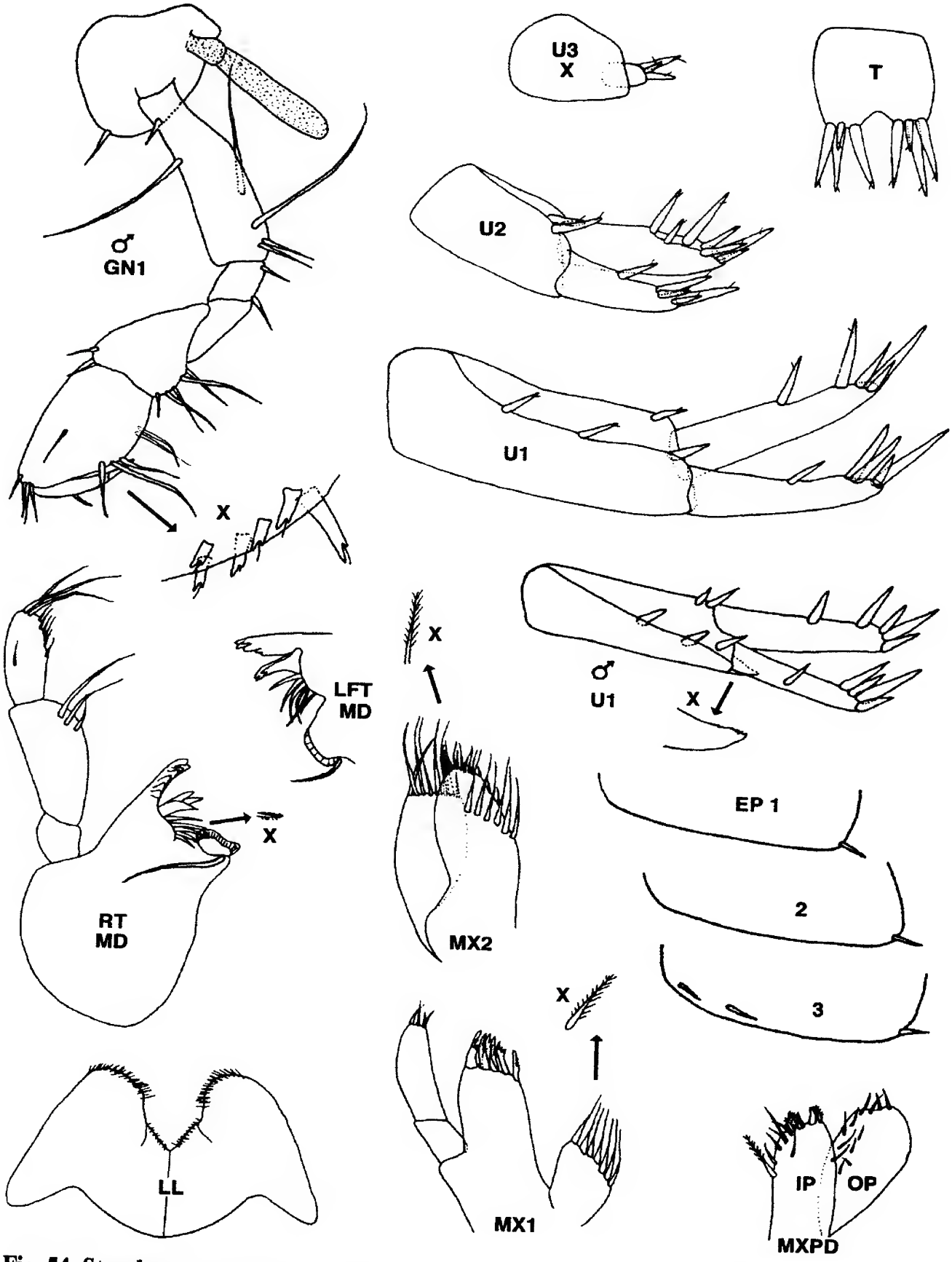

Fig. 54. ***Stygobromus wardi*, n. sp.** Female (3.7 mm); male (3.5 mm). Eagle County, Colorado.

outside, 2 shorter ones on inside; posterior margin without setae; 1 or 2 superior medial setae; 8 - 10 singly inserted inferior medial setae; dactyl nail rather long and sharply pointed; coxa deeper than broad, margin with 1 seta. Gnathopod 2: propod about 2 times longer than broad; palm slightly convex and armed with 19-20 spine teeth in double row; defining angle with 1 long spine tooth on outside, 2 shorter spine teeth on inside; posterior margin about 50 percent length of palm, with 1 set of triply-inserted setae; 3 or 4 superior medial setae; 3 singly-inserted inferior medial setae; coxa about as broad as deep, margin with 4 setae.

Pereopod 3: coxal plate deeper than broad, margin with 2 setae. Pereopod 4: coxal plate relatively broad and deep, reaching about 40 percent length of basis, margin with 4 setae. Pereopod 6 little longer than pereopod 7, about 76 percent length of body, 20 percent longer than pereopod 5. Pereopods 5-7: bases relatively narrow, but little broader proximally than distally; posterior margins weakly convex, not expanded; distoposterior lobes poorly developed, almost indistinct; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 approximately 35 - 40 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Relatively long, simple, lateral sternal gills present on pereonites 6 and 7. Brood plates little expanded distally.

Pleonal plates: posterior margins of plate 1 - 3 weakly convex, with 1 setule near distoposterior corner, distoposterior corners rounded and indistinct; ventral margins of plates 2 and 3 with 2 spines each. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 60 percent length of peduncle, with 9 spines; outer ramus with 6 spines; peduncle with 7 spines. Uropod 2: inner ramus longer than outer ramus, longer than peduncle, with 9-10 spines; outer ramus with 5-6 spines; peduncle with 3 spines. Uropod 3: peduncle usually bearing 2 small setae; ramus approximately 35 percent length of peduncle, with 2-3 apical spines.

Telson little longer than broad, gently tapered distally; apical margin with tiny median notch between spine clusters, bearing 10-12 spines.

Distribution and ecology. This species is known only from a single female. The type locality is one of the longest caves in Colorado (Parris 1973) and contains a stream and lake.

Etymology. The epithet *simplex* is from the Latin, meaning "simple" or "uncomplicated," in reference to the simplicity of a species based on a single specimen.

Stygobromus wardi, new species
(Figs. 53, 54)

Material examined. COLORADO. Eagle Co.: Fulford Cave, S. of Eagle, HOLOTYPE ♀ (USNM 1000076), 3 ♂♂ and 4 ♀♀ paratypes, 1 juv., J. V. Ward and J. R. Holsinger, 6 July 1980; Blue Butt Cave, 6 ♀♀, J. V. Ward and J. R. Holsinger, 6-7 July 1980.

Diagnosis. A small cavernicolous species, morphologically similar to *S. holsingeri* and *S. coloradensis* in structure of gnathopods and uropod 1-2 but distinguished from these species as follows: antenna 1 about 2 times as long as antenna 2; maxillae 1-2 with more setae on inner plate; coxal plates 3-4 broader than deep; bases of pereopods 6-7 with fewer spines on posterior margin; pleonal plates 2-3 with fewer spines on ventral margin; presence of lateral sternal gills (processes); telson broader than deep and with longer apical spines. Largest ♀, 5.0 mm; largest ♂, 3.5 mm.

Female. Antenna 1: 46 percent length of body, approximately 2 times longer than antenna 2; primary flagellum with 18 segments. Antenna 2: flagellum with 5 segments.

Mandibles subequal: spine row with 5-6 plumose spines; palp segment 2 with 3 long setae on inner margin; palp segment 3 bearing 1 B seta, 6 D setae, 3 E setae, lacking A and C setae Inner lobes of lower lip small to vestigial. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 4 stiff setae subapically. Maxilla 2: inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 3 plumose spines, 3-4 naked setae apically, and 1 plumose spine on inner margin; outer plate with 7 or 8 setae on inner margin, 4 setae on or near apex.

Gnathopod 1: propod subequal in size to gnathopod 2; palm straight, approximately same length as posterior margin, armed with 7 spine teeth in double row; defining angle with 2 spine teeth on outside, 2 shorter ones on inside; posterior margin lacking setae; without superior medial setae; 1 - 3 inferior medial setae; dactyl nail rather long; coxa broader than deep, margin with 1 seta. Gnathopod 2: propod longer than broad; palm straight or slightly concave and armed with 8 spine teeth in double row; defining angle with 2 spine teeth of

unequal length on outside, 2 shorter spine teeth on inside; posterior margin little shorter than palm, with 1 set of doubly or triply inserted setae; 3 superior medial setae, one rather long; 2 inferior medial setae; coxa deeper than broad, margin with 1 seta. Pereopod 3: coxal plate deeper than broad, margin with 2-3 setae. Pereopod 4: coxal plate subquadrate, about as broad as deep, reaching about 30 percent length of basis, margin with 3 setae. Pereopod 6 little longer than pereopod 7, about 65 percent length of body, 33 percent longer than pereopod 5. Pereopods 5-7: bases little broader proximally than the distally; posterior margins nearly straight or slightly convex; distoposterior lobes indistinct; anterior and posterior margins with fewer (2-4) spines and setae; segments 4, 5 and 6 of pereopods 5-7 with slender spines; dactyls of pereopods 5-7 relatively slender and elongate, that of pereopod 6 typically up to 40-45 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7; Two pairs of simple lateral sternal gills/processes on pereonites 6 and 7. Brood plates slightly expanded distally.

Pleonal plates: posterior margin of plate 1 convex, with 1 setule near distoposterior corner, that of 2 and 3 less convex, each with 1 setule near distoposterior corner; distoposterior corners rounded; ventral margins of plates 1 and 2 without spines, that of plate 3 with 2 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 5 spines; outer ramus with 5 spines; peduncle with 4 spines. Uropod 2: inner ramus longer than outer ramus, little longer than peduncle, with 7 spines; outer ramus with 5 spines; peduncle with 2 spines. Uropod 3: peduncle without setae; ramus approximately 30 percent length of peduncle, with 3 apical spines.

Telson little broader than long, lateral margins slightly convex; apical margin with shallow median notch between spine clusters, bearing 8 mostly long spines.

Male. Differing from female as follows: gnathopod propods proportionately shorter, palm of propod 2 longer in relation to posterior margin and with fewer teeth. Uropod 1: peduncular process present, reaching about 25 percent length of outer ramus, pointed distally, upper margin minutely serrate; inner ramus with 5 spines; peduncle with 5 spines. Uropod 2: inner ramus with 8 spines, peduncle with 3-4 spines. Telson with 6-9 apical spines.

Distribution and ecology. This species is known only from small streams in two caves in Eagle Co., Colorado, at elevations of approximately 2902 m and 3,048 m (above sea level). It was collected from gravels and assorted rubble in a rapid, high gradient stream in Fulford Cave, one of the larger and better known caves in the state (Parris 1973), where the water temperature was 4.5°C. In Blue Butt Cave, 6 specimens were collected from the silty substrate of the cave stream by a combination of Surber bottom sampler and overnight drift net. A single female (4.0 mm) in the July sample from Blue Butt Cave had 2 large embryos in the brood pouch. The water temperature near the entrance to this cave was 8 °C.

Etymology. This species is named in honor of Prof. Dr. James V. Ward, who helped with the discovery and collection of this species and has made many other significant contributions to the study of subterranean amphipods in Colorado.

Stygobromus species

The following populations were recognized as two distinct species in this study but are not described because of the lack of mature specimens or enough material. These specimens and detailed habitat data were donated by Richard Casey and Gary Byrtus from the Alberta Environmental Center in Vegreville, AB, Canada.

Species No. 1. A single immature male (ca. 4.0 mm), collected by G. Byrtus from a groundwater well on the grounds of the Glencoe Golf and Country Club, just west of Calgary, Alberta, Canada. This species has small, simple lateral sternal gills; telson with small apical notch; uropod 3 with 2 apical spines; and gnathopod 2 larger than gnathopod 1. Its overall morphology is rather typical for species of the hubbsi group with exception of the sternal gills. This specimen was collected along with a second undescribed species, which is listed immediately below (see species no. 2).

Species No. 2. Eleven tiny specimens from: a) groundwater well on grounds of Glencoe Golf and Country Club, just west of Calgary (3 specimens collected by G. Byrtus, 19 Oct. 1993); b) groundwater wells on grounds of Kananaskis Country Golf Course, 60 km west of Calgary (7 apparently immature specimens in 5 samples collected by G. Byrtus from 3 June 1992 to 1 June 1993); c) groundwater well on grounds of Canmore Golf and Curling Club, about 70 km west of Calgary (1 tiny specimen collected by G. Byrtus, 4 May 1993).

PHYLOGENY

A phylogenetic analysis was performed on the 32 morphological characters in Tables 1 and 2, utilizing PAUP 3.1 and MacClade 3.01 (Maddison and Maddison 1993) on a Macintosh computer (OS-7). The choice of characters used in the analysis is based on descriptions from the literature and illustrations. Most characters are binary, but three are multistate. Each series of runs was started with the Heuristic Search option. For the first run, only minimum trees were kept by Random Stepwise Addition, TBR Branch Swapping, and MULPARS options activated. For subsequent runs, all trees in memory from the preceding runs were used, activating MULPARS option and keeping all trees that were as short as, or one step shorter than, those loaded into memory. These steps were repeated until no shorter trees could be found. From the resulting trees, strict and majority rule consensus trees were calculated.

In the first-run, characters were treated as unordered and unweighted (randomly reversible states and equally weighted), assuming that, for example, any number of spines on a certain appendage could evolve directly. In the second run, characters were ordered and partly weighted. Multistate characters were assumed to have evolved in reversible linear transformation series. Some characters were considered more important and were weighted accordingly (see Table 1). In the following discussion, the alternative trees resulting from the analyses are referred to as "unordered-unweighted" and "ordered-weighted." Although the two trees are not identical and have different lengths, there are many similarities between their topologies.

Polymorphic characters, for example, varying numbers of long setae on the inner plate of maxilla 1, were coded according to the scaled method, but not strictly (see Wiens 1995) because the presence of four or five long setae on the inner plate of maxilla 1 could not be treated as two states. In most cases, it would have been more satisfactory to code polymorphic characters in relation to their frequencies. If the majority of the specimens had four long setae, then four setae would be treated as a coded state. However, such information is not always available because some species descriptions are based on an inadequate number of specimens. In this case relevant information of related species is used as a reference.

In some of the species, the occurrence of a character showed a variable or transitional state, for example, the number of apical and subapical spines on the inner ramus of uropod 1 and uropod 2 (e.g., character 25). These variations were treated as separate morphological conditions. Another problem encountered during the analysis was the pronounced degree of interspecific variation. For example, the shape of propod palm of gnathopods 1 and 2 is straight in species A, concave in species B and convex in species C. Two different approaches were used to deal with it. For the first, variable characters were coded as question marks if their morphological/evolutionary significance was not clear. Alternatively, they were coded according to the majority of their frequency occurrence in all species (Wiens 1995).

In our analysis, we chose representative species of three non-stygobromid genera in the family Crangonyctidae as outgroups, including *Synurella ambulans* (central Europe), *Crangonyx forbesi* (east-central North America), and *Bactrurus brachycaudus* (east-central North America). Among the three, only *B. brachycaudus* is a stygobite; the other two species are stygophiles, inasmuch as they are recorded from both surface and subterranean groundwater habitats and are not completely troglomorphic. All three of the outgroup genera share important morphological characters with *Stygobromus*, and their probable phylogenetic relationship to this genus and with other crangonyctids is discussed and illustrated elsewhere (Holsinger 1994a, 1994b).

Assumptions about morphological adaptations of amphipods to subterranean groundwater environments have been discussed in the literature (Stock 1981; Notenboom 1991; Holsinger 1994; Koenemann et al. 1998). Troglomorphisms, such as reduction and/or loss of eyes and pigment and attenuation of certain appendages, which are often treated as apomorphies, are attributed to hypogean adaptation. Alternatively, each corresponding plesiomorphic character state (coded as state 0 in our matrix), may be the condition found in putative surface (epigean) ancestors or relatives of the ancestors. The large number of homoplasies found in amphipod crustaceans tends to severely limit the number of usable or reliable characters available for a cladistic analysis, as well as to impede the choice of effective outgroups. In light of this, our choice of outgroups is probably reasonable, inasmuch as we selected representatives of three of the six extant genera in the family Crangonyctidae, and only one of which is fully adapted morphologically to subterranean waters.

Because the analysis resulted in a relatively large number of cladograms, many of which were very similar, we present two representative 50% majority-

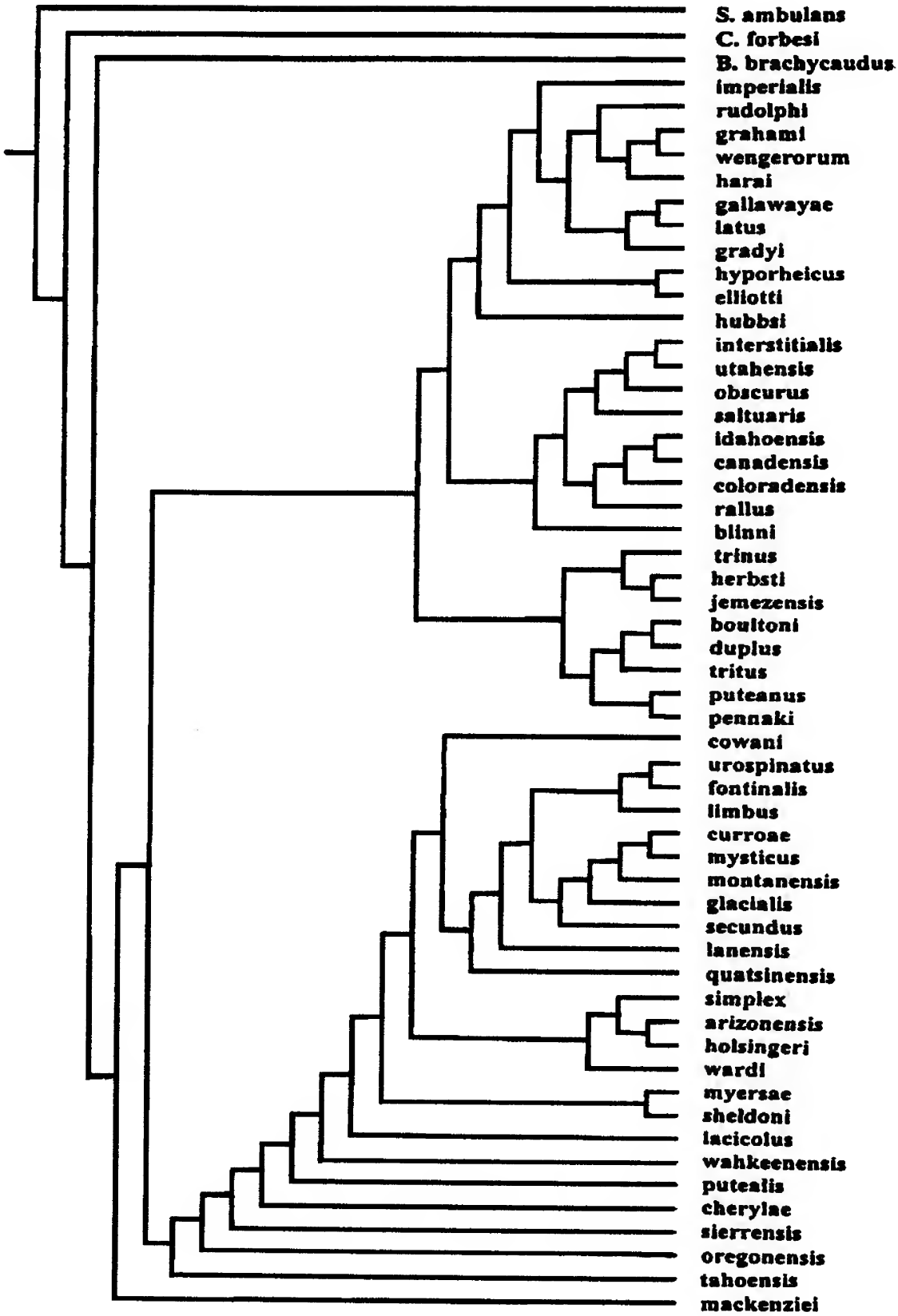

Fig. 55. Majority-rule consensus tree of the first-run using three non-*Stygobromus* species as outgroups; characters not weighted and not ordered (CI: 0.16; RI: 0.50; tree length: 232).

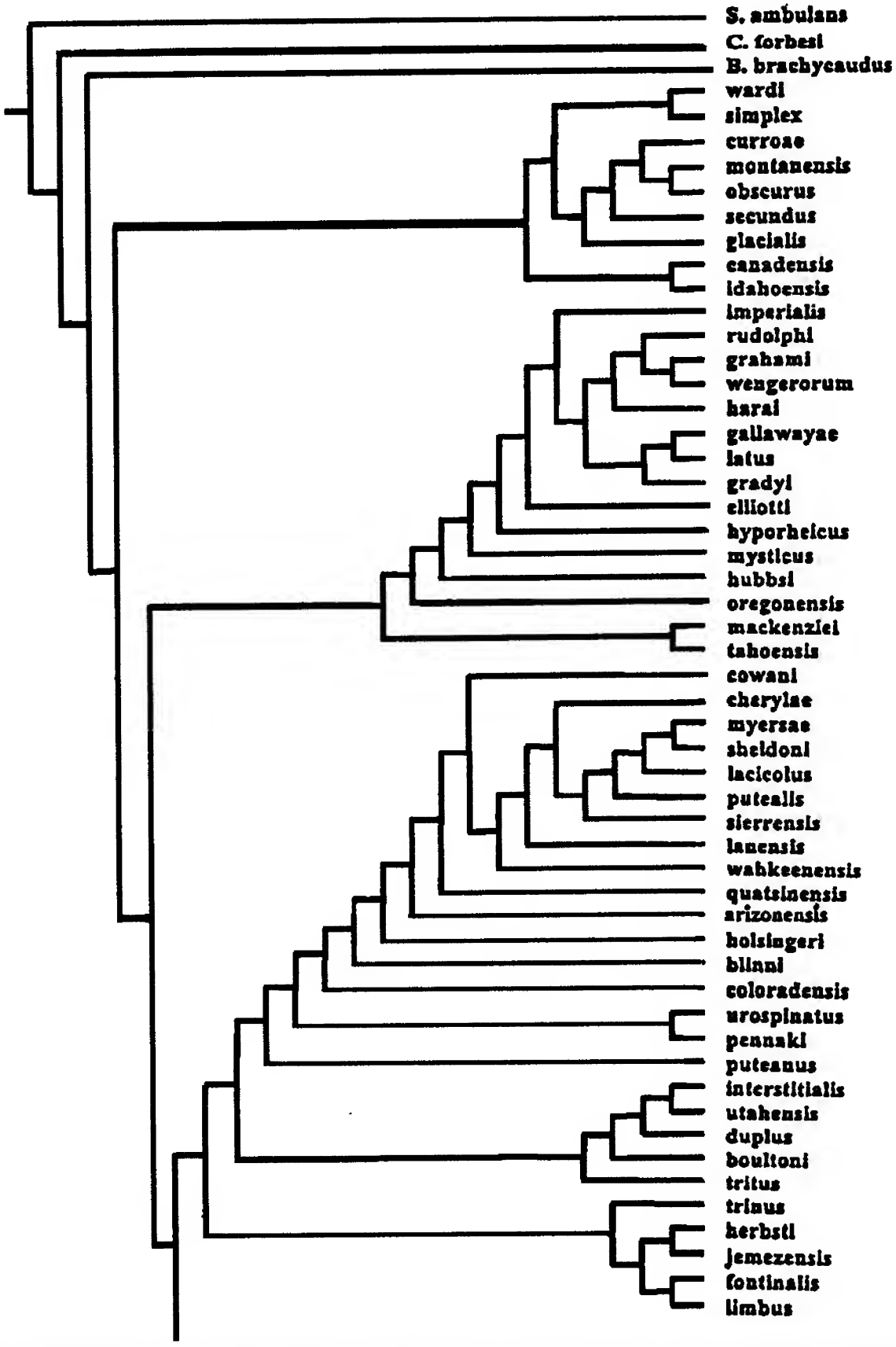

Fig. 56. Majority-rule consensus tree of the second-run using three non-*Stygobromus* species as outgroups; characters partially weighted and ordered (CI: 0.16; RI: 0.51; tree length: 229).

Table 1: List of characters and character states used in the phylonegetic analysis for species of *Stygobromus* in western North America. **Unless otherwise indicated, characters were ordered and weighted by 1 in the second run.**

Antenna

1. Ratio of length of antenna 1 to that of body:
state 0: 50% or less; state 1: more than 50%

Maxillae

2. Plumose setae on inner plate of maxilla 1:
state 0: more than 10; state 1: equal to or less than 10

3. Plumose setae in oblique row on inner plate of maxilla 2:
state 0: more than 11; state 1: equal to or less than 11

Mandibles

4. "B" setae on segment 3 of mandibular palp:
state 0: present; state 1: absent

5. Spines in spine row of mandibles:
state 0: more than 8; state 1: equal to or less than 8

Gnathopods 1 and 2

6. Shape of propod palm of gnathopod 1:
state 0: straight or sinuate; state 1: concave; state 2: convex
The palm shape of the propods of gnathopods 1 and 2 varies in species of *Stygobromus*. The terms straight, concave and convex refer to the general shape of the propod palm. However, the palm of gnathopod 2 may be variably straight or sinuate. Because the distinction between the two is unclear, we treat "straight or sinuate" as a single state.

7. Spine teeth on propod palm of gnathopod 1:
state 0: equal to or less than 28; state 1: more than 28
In second-run: ordered and weighted 2

8. Shape of propod palm of gnathopod 2:
state 0: straight or sinuate; state 1: concave; state 2: convex.
In second-run: ordered and weighted 2.

9: Ratio of length of posterior margin of propod of gnathopod 2 to length of propod palm:
state 0: more than 30%; state 1: 30% or less.

10. Sets of setae, posterior margin of propod, gnathopod 2:
state 0: present; state 1: absent.

11. Coxa of gnathopod 2:
state 0: broader than or approximately as broad as deep
state 1: deeper than broad.

12. Superior medial setae on propod of gnathopod 2:
state 0: present; state 1: absent.

Pereopods

13. Coxa of pereopod 3:
state 0: deeper than or approximately as deep as broad; state 1: broader than deep.

14. Setae on coxal margin of pereopods 3-4:
state 0: equal to or less than 6; state 1: more than 6.

15. Coxa of pereopods 4:
state 0: deeper than or approximately as deep as broad; state 1: broader than deep.

16. Pereopod 6 longer than 7:
state 0: yes; state 1: no.

17. Shape of bases of pereopods 6 and 7:
state 0: normal; state 1: broad
In second-run: ordered and weighted 2.
The term "normal" refers to the ratio of breadth to depth (or length) of the bases seen in most species of *Stygobromus*. However, some species, e.g., *S. duplus, S. rallus* and *S. latus*, have broad bases in comparison with the normal shape .

18. Distoposterior lobe of pereopod 6 and 7:
state 0: present; state 1: absent or indistinct

Sternal Gills/Processes

19. Sternal gill(process):
state 0: present; state 1: absent
In second-runs ordered and weighted 8.
This character plays an important role in separating the species of *Stygobromus* into *hubbsi* group (without sternal gills on pereonites) and non-*hubbsi* species group (with sternal gills on pereonites, typically 6 and 7).

Pleonal plates

20. Setules on posterior margins of pleonal plates 2 and 3:
state 0: 1; state 1: 2 or more.

21. Spines on ventral margin of pleonal plate 3:
state 0: more than 3; state 1: 1-3 ; state 2: absent
In second-run: ordered and weighted 4.

Uropods

22. Some apical spines on inner ramus of uropod 1 nearly as long as that of peduncle:
state 0: no; state 1: yes

23. Spines on peduncle of uropod 1:
state 0: equal to or less than 12; state 1: more than 12.

24. Length of inner ramus of uropod 1 compared to that of peduncle:
state 0: equal to or shorter; state 1: longer.

TABLE 1 (CONT'D).

25. Spines on inner ramus of uropod 2:
state 0: equal to or less than 12. state 1: more than 12.

26. Length of inner ramus of uropod 2 compared with that of peduncle:
state 0: equal to or shorter; state 1: longer.

27. Ratio of length of ramus of uropod 3 to length of peduncle:
state 0: 25% or less; state 1: more than 25%
In second-run: ordered and weighted 3.

28. Spines on apical margin of uropod 3:
state 0: 1-2; state 1: 3 or more.

Telson

29. Apical notch of telson:
state 0: present; state 1: absent or indistinct
In second-run: ordered and weighted 2.

30. Spines on apical margin of telson:
state 0: 8 or less; state 1: more than 8.

31. Apical spines of telson as long as telson:
state 0: no; state 1: yes.

32. Ratio of telson length to width:
state 0: 1.5 times or less; state 1: more than 1.5 times.

rule consensus trees: unordered-unweighted and ordered-weighted (Figs. 55, 56). It is important to note that the consensus trees are very similar in their composition of some clades. For example, both trees support an almost identical monophyletic California-Oregon-Washington clade, consisting of *S. imperialis, S. rudolphi, S. grahami, S. gallawayae, S. latus, S. wengerorum, S. harai, S. gradyi, S. elliotti,* and *S. hubbsi* (Figs. 55, 56). The only difference between the two is the inclusion of *S. mysticus* in the second-run tree (Fig. 56). In addition, the two trees also share three identical doublets, consisting of *S. myersae-S. sheldoni, S. interstitialis-S. utahensis,* and *S. herbsti-S. jemezensis.* However, the ordered-weighted consensus tree appears preferable overall to the alternative unordered-unweighted consensus tree, inasmuch as it supports the monophyly of the hubbsi group and shows a stronger agreement between geographic distribution and terminal taxa (see discussion under Biogeography, below). In establishing the monophly of the *hubbsi* group, the subset of nine western species with sternal gills (processes) becomes an outgroup to the *hubbsi* group species, which completely lack these structures. Undoubtedly, a significant amount of the difference between the trees can be attributed to the added weight given to the absence of sternal gills (see Table 1).

HABITAT DIVERSITY

Species of *Stygobromus* have exploited a wide variety of subterranean groundwater habitats throughout the generic range (Holsinger 1974, 1978; Ward and Holsinger 1981). In western North America, species have been collected from at least four different (generalized) groundwater habitats and deep lakes (Table 3). The groundwater habitats include a) caves, b) springs, c) wells, and d) hypohreic zone. The number of species collected from the five generalized habitat types includes: 19 from caves based on 47 records; 29 from springs based on 53 records; 9 from wells based on 16 records; 9 from hyporheic zones based on 39 records; and 2 from a surface deep lake (Lake Tahoe), based on 15 records.

The generalized aquatic cave habitat actually encompasses three distinctly different, within-cave macrohabitats, including drip/seep pools, streams, and phreatic lakes, but these are not differentiated *per se* in Table 3. Springs generally represent the resurgence of groundwater at the surface, although some may be seep-like, with intermittent flow contingent on seasonal precipitation and elevation of the groundwater table. Some seeps, however, are recognized as a distinct groundwater habitat called the hypotelminorheic. Wells are more of a means of access to groundwater aquifers than a habitat *per se.* They usually consist of conventional domestic water wells but sometimes include PVC pipes driven into the substrate of a surface stream or into a nearby phreatic aquifer. The hyporheic habitat is defined as the underflow of groundwater beneath surface streams and is accessed either by pumping water though PVC pipes or sampling directly into the gravel substrate of the stream. Thus, the difference in habitat for amphipods collected from a well of the PVC type or directly from the hyporheic zone is not always clear. A surface deep lake is not a typical groundwater habitat, although two species of *Stygobromus* are recorded from Lake Tahoe in western North America (Holsinger 1974) and one from a deep lake in Siberia (Holsinger 1987). It is assumed that these species probably gain access to lake waters via groundwater seeps developed in the walls or floor of the lake basin.

With respect to the number of cave-dwelling species, there is a significant contrast between the eastern and western North American stygobromid fauna. In a

Table 2. Character data matrix (question marks refer to unknown character states).

	Taxon/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	*B. brachycaudus*	1	0	0	0	0	2	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	*C. forbesi*	0	1	0	0	1	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0
3	*S. ambulans*	1	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
4	*imperialis*	1	1	1	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
5	*cowani*	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	1	1	1	0	0	0	0	1	0	0	0	1	0	0
6	*trinus*	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0
7	*hyporheicus*	1	0	0	1	0	2	1	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	0	1
8	*rudolphi*	1	1	1	0	1	0	0	1	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0
9	*gallawayae*	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0
10	*cherylae*	1	0	0	0	1	2	0	0	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	1	1	0	0
11	*myersae*	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1
12	*herbsti*	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	1	0	1	1	0	1	0	0
13	*urospinatus*	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	1	0	1	1	0
14	*fontinalis*	1	0	1	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	1	?	?	0	0	0	1	1	0	1	0	1	0	0
15	*interstitialis*	1	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	2	1	0	0	0	0	1	0	0	1	1	0
16	*wardi*	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	?	?	0	0	0	0	1	0	1	0	1	1	0
17	*blinni*	1	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	1	?	?	0	0	0	0	0	0	0	0	1	0	0
18	*jemezensis*	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0
19	*lanensis*	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	1	0	1	0	0
20	*wahkeenensis*	1	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	1	0	1
21	*rallus*	1	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0
22	*latus*	1	1	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0	1	0	1	1	1	0	1
23	*utahensis*	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	1	0	0
24	*limbus*	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1
25	*boultoni*	1	0	0	0	1	1	0	1	1	1	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	0
26	*hubbsi*	0	0	0	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0
27	*tritus*	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	0
28	*puteanus*	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	0	0	0	1	1	1	1	1	0
29	*oregonensis*	0	0	0	0	1	0	1	0	0	0	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0
30	*elliotti*	1	1	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1	1	0	1
31	*grahami*	1	1	1	0	1	0	0	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0
32	*gradyi*	1	1	1	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0
33	*harai*	0	1	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0
34	*wengerorum*	1	1	1	0	1	2	0	1	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1
35	*mackenziei*	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
36	*sierrensis*	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	1	0	0
37	*sheldoni*	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1
38	*tahoensis*	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0
39	*lacicolus*	0	0	0	0	1	0	0	1	1	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	1	0	1
40	*arizonensis*	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	1	0	0
41	*pennaki*	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	1	0	1	0	0	1	0	1	1	0
42	*coloradensis*	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0
43	*holsingeri*	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	1	1	0
44	*putealis*	0	0	0	1	1	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	1	1	0	1
45	*duplus*	1	0	0	1	1	2	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	0
46	*saltuaris*	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0
47	*quatsinensis*	1	0	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	1	0	0
48	*mysticus*	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1
49	*canadensis*	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0
50	*currooe*	1	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	?	?	0	0	0	1	1	0	0	0	1	0	1
51	*glacialis*	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0
52	*idahoensis*	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	1	1	1	0
53	*montanensis*	1	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0
54	*obscurus*	1	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	1	0	1	1	0
55	*secundus*	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0
56	*simplex*	0	0	0	0	1	2	0	2	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0

Note: *Bactrurus brachycaudus*, *Crangonyx forbesi* and *Synurella ambulans* are outgroup species.

study of 48 species of *Stygobromus* from eastern North America, primarily from the Appalachians and Coastal Plain (Holsinger 1978), 41 species were recorded from caves, whereas in the present study of 53 species from western North America (including one from wells in Wisconsin), only 21 species are reported from caves. Moreover, in the east approximately 63 percent of the records of *Stygobromus* are from caves and approximately 21 species are known only from caves. In comparison, in the west approximately 28 percent of the records are from caves and approximately 16 species are known only from caves. This significant regional difference may well be explained by the availability of cave habitats. On a broad scale, the number, as well as density, of caves is many magnitudes greater in eastern North America than in western North America. Conversely, there are 39 (+) records for nine species of *Stygobromus* from the hyporheic habitat in western North America, whereas there are very few records for species of *Stygobromus* from hyporheic habitats in eastern North America. The gravel substrates of many river systems in the west appear to be rich in exploitable interstitial spaces, which are in turn essential to hyporheic habitat structure.

BIOGEOGRAPHY

As shown on the maps in figures 57-61, the geographic distribution of 53 species of *Stygobromus* in western North America (including *S. putealis* from Wisconsin) is widespread and scattered, although distinct clusters of species occur in north-central California, western Oregon-southern Washington, northwestern Montana-southern Alberta, and north-central Colorado. Many of these species display highly insular ranges, and 24 are currently known only from single localities. Moreover, with the notable exception of *S. quatsinensis* (see Holsinger et al. 1997), those species recorded from more than one locality are restricted to small ranges.

Taxonomic diversity, based on number of species groups, and species richness within the genus *Stygobromus* are significantly greater in North America east of the Great Plains than in the in North America west of the Great Plains (Holsinger 1986b). That these two regions are generally comparable in size and are occupied by species of the same genus tends to justify this comparison. In the east, approximately 94 species are either described (ca. 72) or are in the process of being described (descriptions of 22 in ms.), and most of them can be assigned to one of approximately 16 species groups. However, in the west there are 52 described species, 44 of which are assigned to the *hubbsi* group. The remaining nine species, excepting *S. canadensis* which appears to represent a distinct group (Holsinger 1980), are not assigned to a group. Moreover, except for the presence of sternal gills, several of the nine non-*hubbsi* group species are similar morphologically to members of the *hubbsi* group.

A two-fold hypothesis was proposed earlier (Holsinger 1986b) to explain the reduced taxonomic diversity in this region vis-a-vis the significantly greater diversity in a comparable-sized part of eastern North America, and to account for the geographic distribution of numerous, morphologically closely similar stygobitic species of *Stygobromus* over a large part of the geologically variable terrane of the western Cordillera of North America.

First, many physiographic regions in eastern and central United States with large numbers of species, such as the Appalachians, Interior Low Plateaus, Ozarks, and Edwards Plateau, are characterized locally by extensive karst terranes that contain numerous cave and subterranean groundwater habitats. In contrast, karst terranes in western North America are greatly limited in extent, and cave density is much lower. Thus, the availability of karst groundwater habitats is significantly less in western North America and has undoubtedly played a major role in limiting the diversity of *Stygobromus* species. The difference in the geological history of the two regions has also been important, inasmuch as potential habitats in the west probably developed more recently than those in the east because of the pronounced tectonic activity in the western Cordillera since the middle Cenozoic. In contrast, geological activity in the east during the same time frame has been relatively stable, allowing the existence of comparatively older and less perturbed habitats. The more humid climate of eastern North America would also enhance the development and recharge of groundwater aquifers, whereas in the west, the overall drier climate would not be as favorable to recharge.

Second, the comparative lack of taxonomic diversity in the west may also be a reflection of the pronounced geological activity in the Cenozoic which, in turn, is largely responsible for the relative youth of groundwater habitats in this regiion. The widespread distribution of so many closely similar species of *Stygobromus* suggests that they may be derived from a relatively recent, widely distributed ancestor. The recent, rapid, and often violent development of present landforms in the west during the Cenozoic would have

Table 3. Records of species of *Stygobromus* from five kinds of generalized habitats in western North America.

Species	caves[1]	springs	wells[2]	hyporheic[3]	deep lake[4]
arizonensis	3	1	-	-	-
blinni	1	-	-	-	-
boultoni	-	-	2	-	-
canadensis	1	-	-	-	-
cherylae	-	1	-	-	-
coloradensis	-	-	-	10(+)	-
cowani	-	1	-	-	-
currodae	-	-	-	1	-
duplus	-	-	2	-	-
elliotti	3	-	-	-	-
fontinalis	-	2	-	-	-
gallawayae	-	1	-	-	-
glacialis	3	-	-	-	-
grahami	8	-	-	-	-
gradyi	4	-	-	-	-
harai	3	1	-	-	-
herbsti	-	10	-	-	-
holsingeri	-	1	-	10(+)	-
hubbsi	1	-	-	-	-
hyporheicus	-	-	-	1	-
idahoensis	-	-	-	1	-
imperialis	1	-	-	-	-
interstitialis	-	-	-	3	-
jemezensis	-	-	1	-	-
lacicolus	-	-	-	-	5
lanensis	-	1	-	1	-
latus	-	6	-	-	-
limbus	1	-	-	-	-
mackenziei	1	-	-	-	-
montanensis	-	-	1	-	-
myersae	-	3	-	-	-
mysticus	-	-	1	-	-
obscurus	-	-	1	-	-
oregonensis	1	-	-	-	-
pennaki	-	-	-	10(+)	-
*putealis**	-	-	5	-	-
puteanus	-	-	1	-	-
quatsinensis	9	8	-	-	-
rudolphi	-	1	-	-	-
rallus	-	5	-	-	-
saltuaris	-	-	-	1	-
sierrensis	-	1	-	-	-
sheldoni	-	5	-	-	-
secundus	-	1	-	-	-
simplex	1	-	-	-	-
tahoensis	-	-	-	-	10
trinus	1	-	-	-	-
tritus	-	-	2	-	-
urospinatus	-	3	-	-	-
utahensis	1	-	-	-	-
wardi	2	-	-	-	-
wengerorum	2	-	-	-	-
wahkeenensis	-	1	-	-	-

1- Includes 1 mine record each for *S. arizonensis* and *S.harai* and caves in limestone or basalt for all others; 2- Includes PVC wells driven into stream beds; 3- Includes interrupted streams for *S. holsingeri*; 4- Includes only 2 species from Lake Tahoe (precise habitat is unknown).
*This species is recorded from Wisconsin.

fragmented the range of a widespread, ancestral groundwater species into numerous isolated populations, ultimately resulting in the evolution of the many scattered but closely similar species (Holsinger 1974). In comparison, species of *Stygobromus* in eastern North America living in groundwater habitats developed in geologically older and more stable terranes probably have a longer evolutionary history, which would, in turn, account for their greater taxonomic diversity.

The occurrence of *S. putealis* in southeastern Wisconsin just east of the Driftless area (Fig. 57) may give us a better idea of the age and former potential distribution of the *hubbsi* group or its immediate ancestor. The occurrence of this species approximately 1400 km east of the western Cordillera is strong evidence of a former continuous distribution of the *hubbsi* group or its immediate past ancestor across what is now the Great Plains (Holsinger 1986b). The present disjunction between *S. putealis* and related species in the west may well have developed through progressive aridity in the Miocene or destruction of groundwater habitats by glaciation in southern Canada or the northern United States during the Pleistocene. Whichever is the correct explanation for the disjunction, it is probable that a continuous distribution of the *hubbsi* group across the Great Plains is at least as old as the early Pleistocene or even as old as the Miocene.

The pluvial lake system of the Pleistoecene might have potentially affected the former distribution of some species of the *hubbsi* group. It is well established that an extensive pluvial lake system existed in parts of the western Cordillea during glacial maxima of the Pleistocene, which would have effected elevation of groundwater tables and expansion of groundwater aquifers. However, most of these lakes were developed in parts of the Basin and Range and Columbia Plateau and would potentially have impacted the distribution of relatively few species of *Stygobromus*. The majority of species occur the mountainous areas to the east and west of the provinces with most of the pluvial lakes.

To obtain a better picture of the relationship between the taxa (species) and their geographic distributions, we converted the taxon cladogram in Figure 56 to the taxon-area cladogram in Figure 62 by substituting areas for terminal taxa (species). The areas are major physiographic provinces of western North America, and the rationale for using them as areas is because each is defined by its unique geomorphogy, climate, and historical geology. Moreover, each area has endemic species that are so far unrecorded in any other area, although one exception may be *S. pennaki*, which has been recorded from one locality just outside the Southern Rocky Mountain area on the extreme western margin of the Great Plains (Fig. 59).

Within the *hubbsi* group, the strongest agreement between taxa and areas is the large clade of 15 species (extending from *tahoensis* to *imperialis* on the cladogram), which occurs in the western part of the region. These species are recorded from the Coastal Range, Cascades, Sierra Nevada, and Columbia Plateau. Moreover, a strong nested subset within this clade is composed of *S. grahami*, *S. harai*, and *S. wengerorum*, which live in caves in the Mother Lode region of eastern California (see also Holsinger 1974), and *S. rudolphi* from a spring to the southwest in the Coastal Range. Ten of these 15 species make up the monophyletic California-Oregon-Washington clade discussed under Phylogeny, above. A second reasonably strong clade is also found in the western part of the region and consists of eight species from the Coastal Range, Sierra Nevada and Cascades (species extending from *S. quatsinensis* to *S. cherylae* on the cladogram). However, this clade is not fully congruent geographically, inasmuch as it also contains *S. myersae* from just east of the the Sierra Nevada in the Basin and Range, and more importantly, *S. putealis* from Wisconsin. The fact that *S. putealis* is imbedded in the middle of the cladogram is a further indication that this species, despite its huge geographic separation from the western Cordillera, is a bona fide member of the *hubbsi* group.

Almost all remaining species on the cladogram are recorded from the central and eastern parts of the western Cordillera and occur in different sections of the Rocky Mountains, Colorado Plateaus, Basin and Range, and one in the Great Plains (just east of the Basin and Range in far western Texas). The position of *S. trinus*, *S. rallus*, and *S. saltuaris* on the cladogram (Fig. 62) is unclear and incongruent with geographic distribution. However, it is clear that the *hubbsi* group species appear to be split roughly into eastern and western subsets on opposite sides of the Basin and Range-Columbia Plateau (see Figs. 59-61). Twenty-three species are recorded from the Cascades-Sierras Nevada-Coastal Range on the western side of the Cordillera, and 20 species are recorded from the Rocky Mountains and Colorado Plateau on the eastern side. However, only seven species are recorded from the Basin and Range-Columbia Plateau and four of them occur near the edge of this combination of provinces. The extreme aridity that has developed throughout

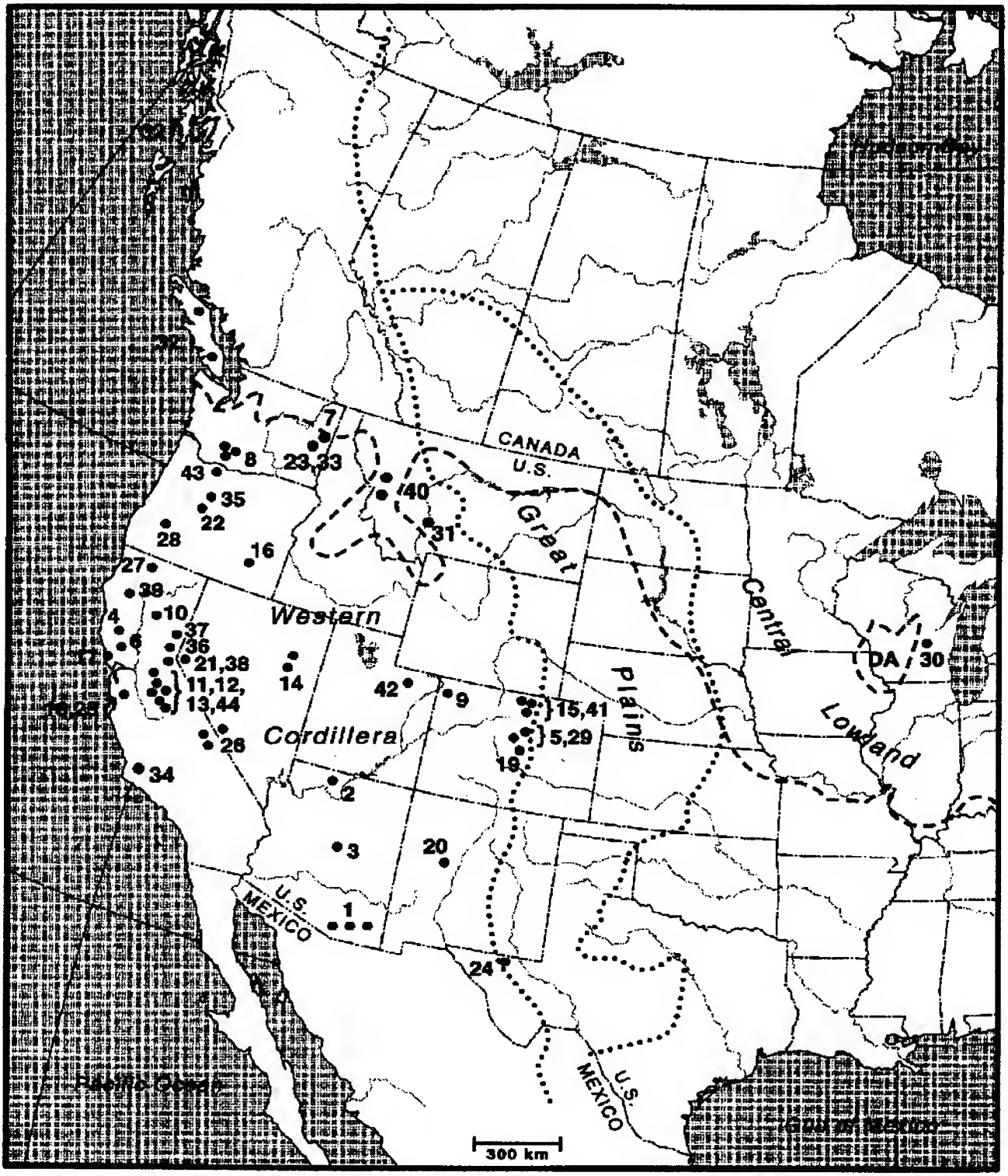

Fig. 57. Geographic distribution of 44 species of *Stygobromus* in the *hubbsi* group in North America. A closed circle indicates one to many closely proximate locality records for a species. 1, *S. arizonensis*; 2, *S. blinni*; 3, *S. boultoni*; 4, *S. cherylae*; 5, *S. coloradensis*; 6, *S. cowani*; 7, *S. duplus*; 8, *S. elliotti*; 9, *S. fontinalis*; 10, *S. gallowayae*; 11, *S. gradyi*; 12, *S. grahami*; 13, *S. harai*; 14, *S. herbsti*; 15, *S. holsingeri*; 16, *S. hubbsi*; 17, *S. hyporheicus*; 18, *S. imperialis*; 19, *S. interstitialis*; 20, *S. jemezensis*; 21, *S. lacicolous*; 22, *S. lanensis*; 23, *S. latus*; 24, *S. limbus*; 25; *S. mackenziei*; 26, *S. myersae*; 27, *S. mysticus*; 28, *S. oregonensis*; 29, *S. pennaki*; 30, *S. putealis*; 31, *S. puteanus*; 32, *S. quatsinensis*; 33, *S. rallus*; 34, *S. rudolphi*; 35, *S. saltauris*; 36, *S. sheldoni*; 37, *S. sierrensis*; 38, *S. tahoensis*; 39, *S. trinus*; 40, *S. tritus*; 41, *S. urospinatus;* 42; *S. utahensis*; 43, *S. wahkeenensis*; 44, *S. wengerorum*. See figs. 59-61 for greater detail. The heavy dashed line represents the approximate southern extent of Pleistocene glaciation. DA = the Wisconsin Driftless Area.

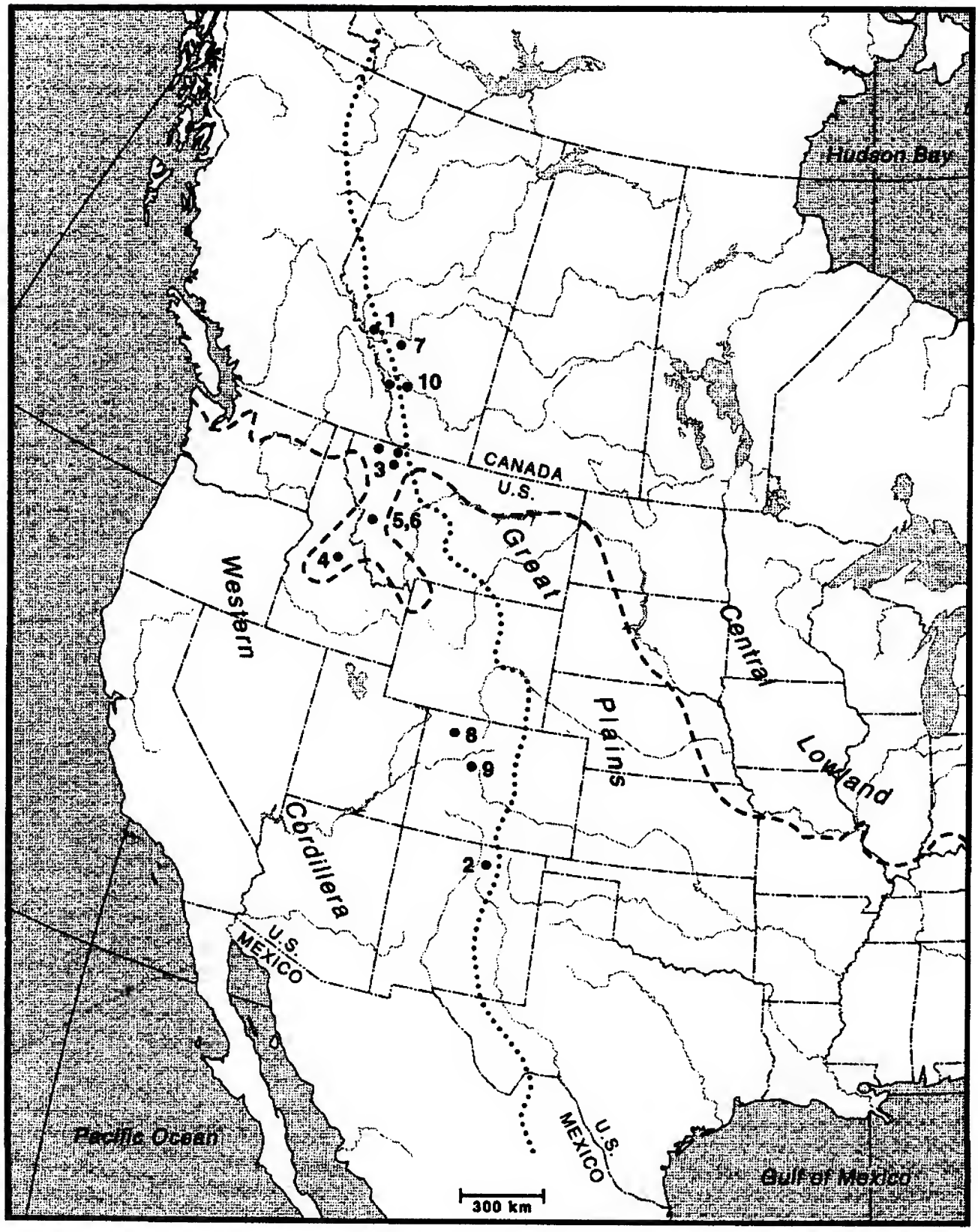

Fig. 58. Geographic distribution of non-*hubbsi* group species of *Stygobromus* in the western Cordillera of North America: 1, *S. canadensis;* 2, *S. currorae;* 3, *S. glacialis;* 4, *S. idahoensis;* 5, *S. montanensis;* 6, *S. obscurus;* 7, *S. secundus;* 8, *S. simplex;* 9, *S. wardi*; 10, specimens of 1 or 2 new species of *Stygobromus* from 3 localities west of Calgary that cannot be described without additional material. See figs. 59 and 60 for greater detail. The heavy dashed line represents the approximate southern extent of Pleistocene glaciation.

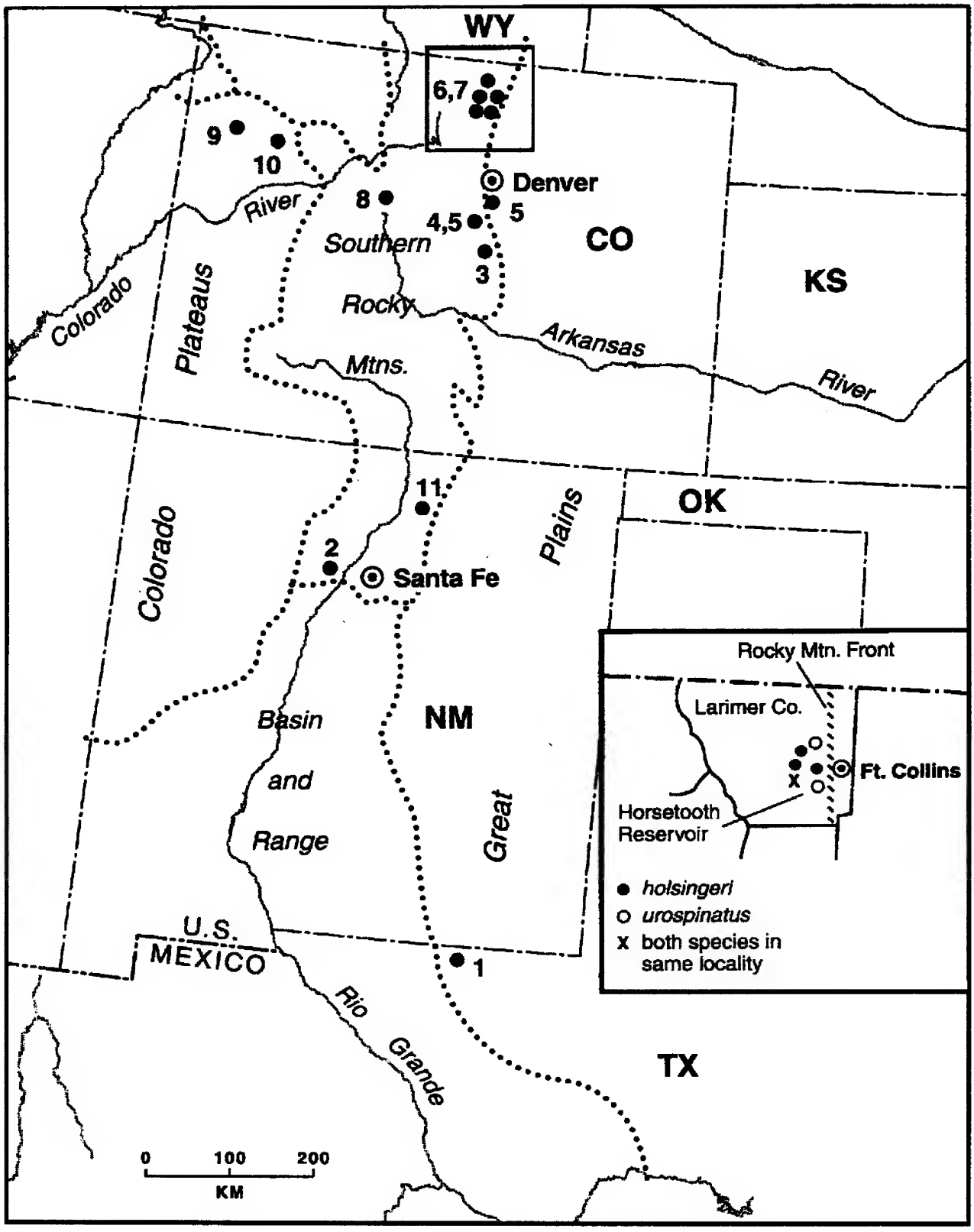

Fig. 59. Geographic distribution of *Stygobromus* in Colorado, New Mexico and far western Texas. A closed circle indicates one to many closely proximate localities for a species (number of recorded localities in parentheses). Hubbsi group: *S. limbus* (1 loc.); 2, *S. jemezensis* (1 loc.); 3, *S. interstitialis* (3 locs.); 4, *S. coloradensis* (8 or 9 locs.); 5, *S. pennaki* (7 or 8 locs.); 6, *S. holsingeri* (approx. 25 locs.); 7, *S. urospinatus* (3 locs.); 8,; 9, *S. fontinalis* (2 locs.). Other species: 9, *S. wardi* (2 locs.); 10, *S. simplex* (1 loc.); 11, *S. curroae* (1 loc.). Insert: closed circles, *S. holsingeri*; open circles, *S. urospinatus*; x, both species from same locality.

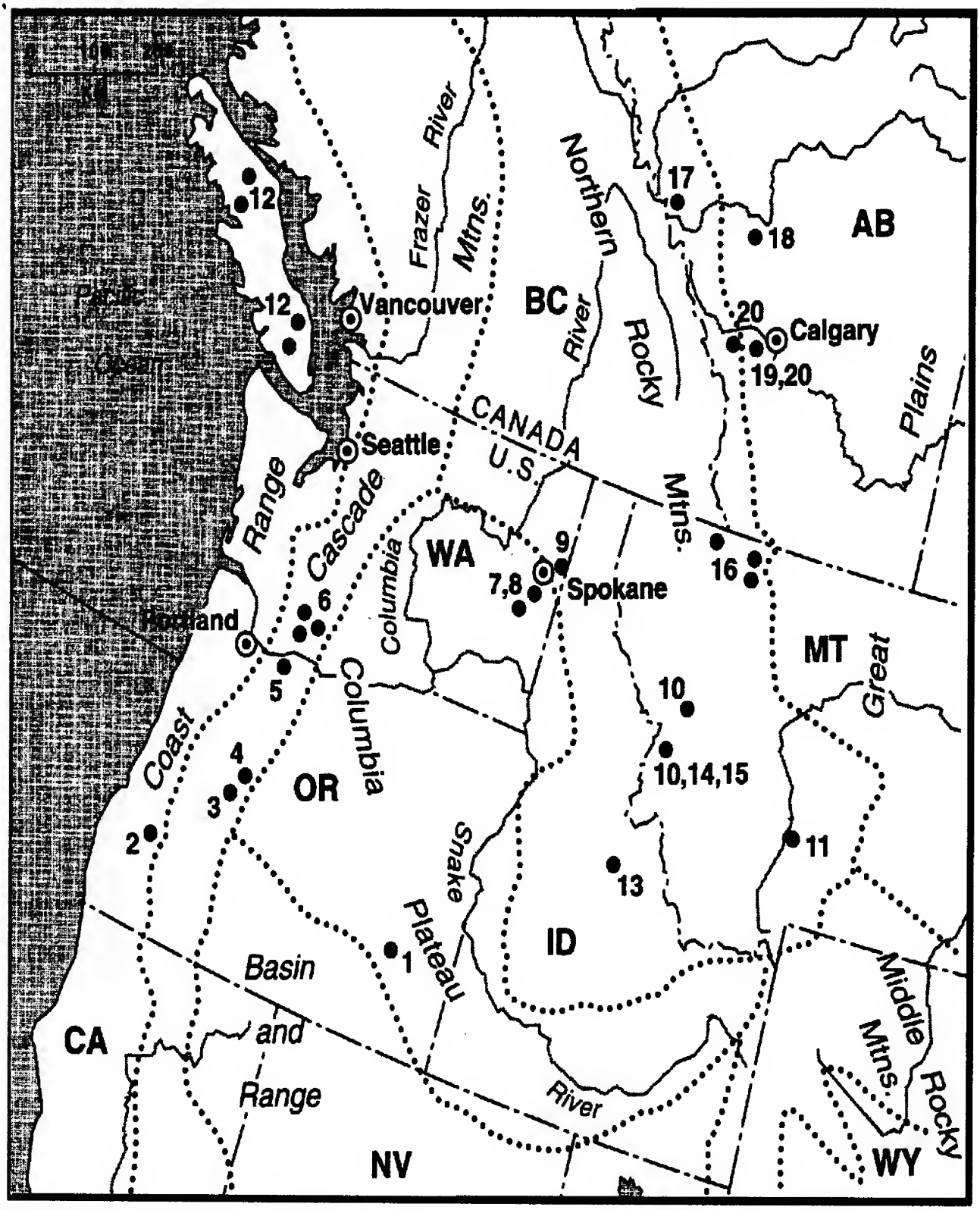

Fig. 60. Geographic distribution of *Stygobromus* in Idaho, Montana, Oregon, and Washington, USA; and Alberta and British Columbia, Canada. A closed circle indicates one to several closely proximate localities for a species (number of recorded localities in parentheses). *hubbsi* group: 1, *S. hubbsi* (1 loc.); 2, *S. oregonensis* (1 loc.); 3, *S. lanensis* (1 loc.); 4, *S. saltauris* (1 loc.); 5, *S. wahkeenensis* (2 locs.); *6, S. elliotti* (3 locs.); 7, *S. latus* (3 locs.); 8, *S. rallus* (2 locs.); 9, *S. duplus* (2 locs.); 10 *S. tritus* (2 locs.); 11, *S. puteanus* (1 loc.); 12, *S. quatsinenesis* (4 localities on Vancouver Island; 26 in southeastern Alaska not shown). Other species: 13, *S. idahoensis* (1 loc.); 14, *S. montanensis* (1 loc.); 15, *S. obscurus* (1 loc.); 16, *S. glacialis* (3 locs.); 17, *S. canadensis* (1 loc.); 18, *S. secundus* (1 loc.); 19 & 20, S. spp.(2).

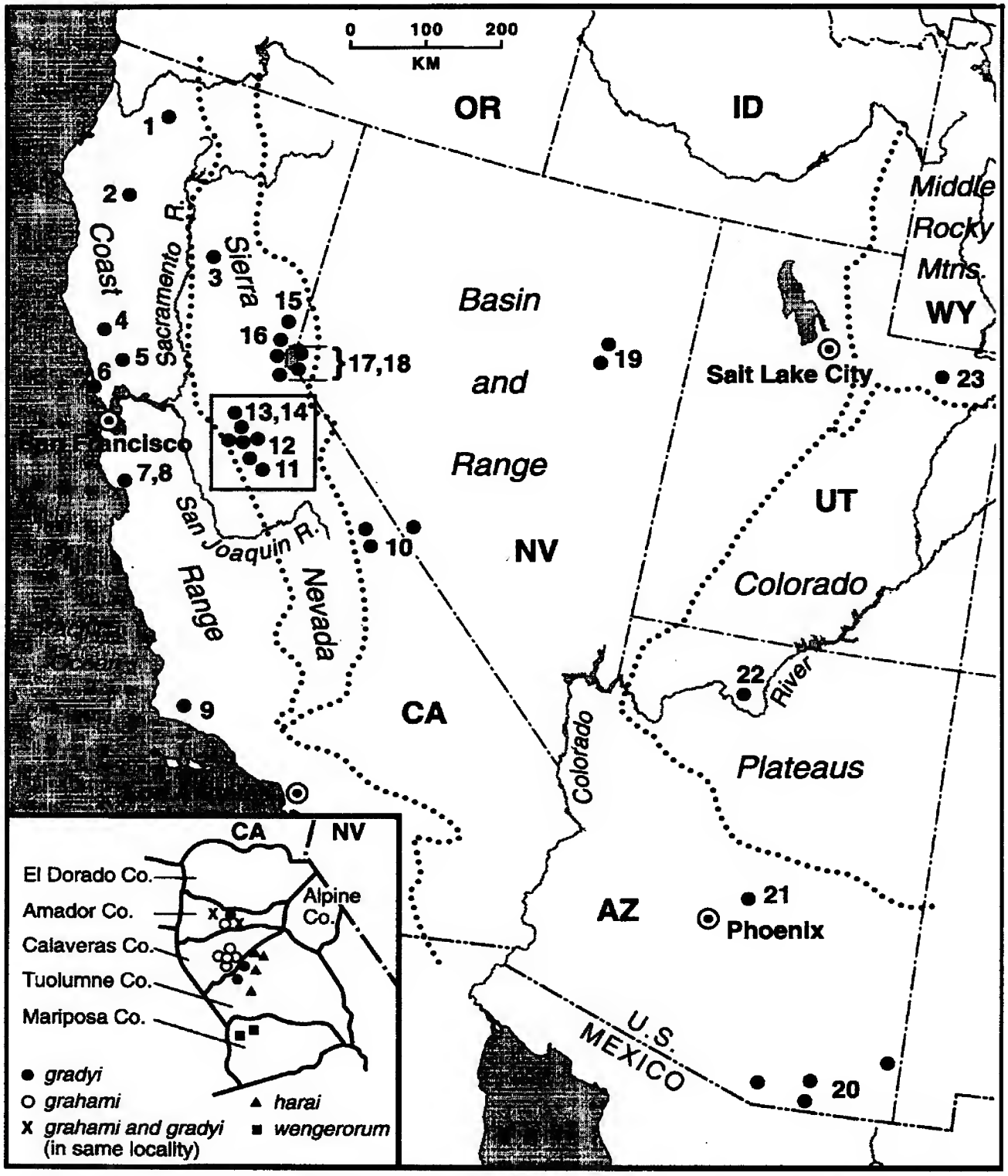

Fig. 61. Geographic distribution of *Stygobromus* in Arizona, California, Nevada and Utah. A closed circle indicates one to several closely proximate localities for a species (number of recorded localities in parentheses). *lubbsi* group: 1, *S. mysticus* (1 loc.); 2, *S. trinus* (1 loc.); 3, *S. gallowayae* (1 loc); 4, *S. cherylae* (1 loc.); 5, *S. cowani* (1 loc.); 6, *S. hyporheicus* (1 loc.); 7, *S. imperialis* (1 loc.); 8, *S. mackenziei* (1 loc.); 9, *S. rudolphi* (1 loc.); 10, *S. myersae* (3 locs.); 11, *S. wengerorum* (2 locs.); 12, *S. harai* (4 locs.); 13, *S. grahami* (8 locs.); 14, *S. gradyi* (5 locs.); 15, *S. sierrensis* (1 loc.); 16, *S. sheldoni* (4 or 5 locs.); 17, *S. tahoensis* (9 or 10 sites in Lake Tahoe); 18, *S. lacicolous* (5 sites in Lake Tahoe); 19, *S. herbsti* (10 locs.); 20, *S. arizonensis* (4 locs.), 21, *S. boultoni* (2 locs.); 22, *S. blinni* (1 loc.); 23, *S. utahensis* (1 loc.). Insert: open circles, *S. grahami*; closed circles, *S. gradyi*; x, localities with both *S. grahami* and *S. gradyi;* closed triangles, *S. harai; closed boxes, S. wengerorum.*

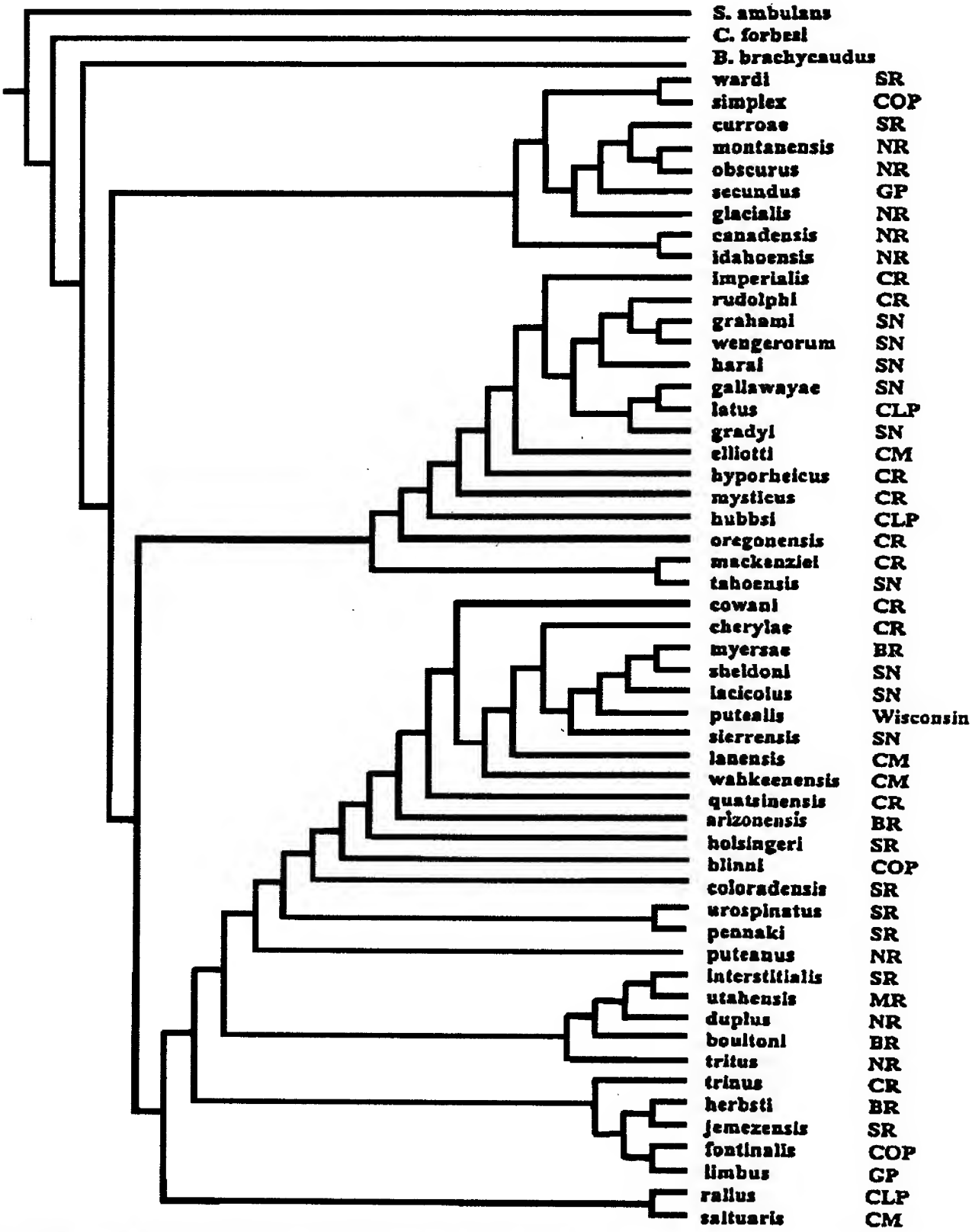

Fig. 62. Taxon-area cladogram converted from the majority-rule consensus tree in Fig. 56. Areas (see text) (with their number of species in parentheses) are as follows: Basin and Range (BR) (4 spp.); Colorado Plateaus COP (3 spp.); Northern Rocky Mountains NR (8 spp.); Middle Rocky Mountains (MR) (1 sp.); Southern Rocky Mountains (SR) (8 spp.); Columbia (Lava) Plateau (CLP) (3 spp.); Cascade Mountains (CM) (4 spp.); Sierra Nevada Mountains (SN) (9 spp.); Coastal Range (CR) (10 spp.); Great Plains (GP) (2 spp.); and Wisconsin (1 sp.).

much of the Basin and Range and Columbia Plateau since the Pleistocene (see Minckley et al. 1986) has probably led to the development of dispersal barriers for groundwater amphipods and contributed to physical isolation of species of the *hubbsi* group to opposite sides.

It is also important to note that all of the nine non-*hubbsi* group species occur on the eastern side of the western Cordillera and that six of them are recorded from areas that were glaciated or were in close proximity to glaciation during the Pleistocene. Although some of these species appear to occupy a position close to the ancestor(s) of the *hubbsi* group, others, such as *S. canadensis*, may not.

ADDENDUM

Subsequent to this study and during the last phase of manuscript preparation, a significant number of amphipod samples from groundwater habitats or groundwater-associated habitats in western North America were sent to JRH for determination. Although it was too late to include a detailed study of this material in the present paper, a very brief summary will be made. These samples were collected from approximately 22 different localities in five different states and appear to represent approximately 11 undescribed species of *Stygobromus*, some of which can be assigned to the *hubbsi* group, and one possibly to a new crangonyctid genus. The collections were made in the following localities by the persons indicated in parentheses: 3 sites (stream sediments) in Santa Clara County (Steve Fend) and a spring in Somona County (C. B. Barr and W. D. Shepard), California; 1 site (hyporheic ?) in Boise County, Idaho (Gary Lester ?); hypohreic and deep lake sites in Jackson, Josephine and Klamath counties, Oregon (R. W. Wisseman); 2 springs and 1 cave in Cache County, Utah (Candace Brindza); hyporheic habitats in Queets River, Olympic National Park, Jefferson County (Holly Coe) and East Lakes, Cascades National Park, Whatcom County (Amy Hill), Washington. In addition, undetermined species of *Stygobromus*, one of which is apparently *S. glacialis*, are reported by Stanford et al. (1994) and J. V. Ward (pers. comm.) from groundwater habitats in the Flathead River catchment in northwestern Montana.

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Legend for Figures

A1,2	-	antennae 1, 2
ABD	-	abdomen
BR PL	-	brood lamella
CX	-	coxal plate
EP 1,2,3	-	abdominal side plates 1, 2, 3
GN1, 2	-	gnathopods 1, 2
HD	-	head
IP	-	inner plate
LFT	-	left
LL	-	lower lip (labium)
MD	-	mandible
MX1	-	maxilla 1
MX2	-	maxilla 2
MXPD	-	maxilliped
OP	-	outer plate
P3-7	-	peraeopods 3, 4, 5, 6, 7
PLP	-	pleopod
RT	-	right
T	-	telson
U1,2,3	-	uropods 1, 2, 3
UL	-	upper lip (incl. epistome)
X	-	part enlarged
♂	-	male
♀	-	female

Note: All appendages are those of the female specimen, unless preceded by the male (♂) symbol. Individual appendages are enlarged to visually suitable scales.